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ANNALS

OF THE

MISSOURI BOTANICAL GARDEN

TABLE OF CONTENTS

	PAGE
Flora of Panama. Part V, Fascicle 1 (Lauraceae to Cruciferae) ... Robert E. Woodson, Jr., Robert W. Schery and collaborators	1–106
A Dicotyledonous Wood Found Associated with the Idaho Tempskyas ... William Spackman, Jr.	107–115
The Uses of Hevea for Food in Relation to Its Domestication ... R. J. Seibert	117–121
The Use of Glands in a Taxonomic Consideration of the Family Bignoniaceae ... R. J. Seibert	123–136
Gynandropsis, Cleome, and Podandrogyne ... Robert E. Woodson, Jr.	139–146
Maize in the Great Herbals ... John J. Finan	149–191
Contributions to Our Knowledge of American Carboniferous Floras. X. An Osmundaceous Stem from Iowa ... Henry N. Andrews and Robert W. Baxter	193–201
A Crossotheca from Northern Illinois ... Henry N. Andrews and Sergius Mamay	203–204
A Note on *Fomes idahoensis* Brown ... Henry N. Andrews	207
A Study of the Vegetative Anatomy of the Genus Sphenophyllum from American Coal Balls ... Robert W. Baxter	209–231
Miscellaneous New Apocynaceae and Asclepiadaceae ... Robert E. Woodson, Jr.	233–238
Quantitative Determination of the Pigment Content of Single Cells by Means of a New Microspectrophotometer ... Barry Commoner	239–254
The Southern Dent Corns ... William L. Brown and Edgar Anderson	255–268
The 1947 Conference on the Inflorescences of *Zea Mays:*	
Ear and Tassel Development in Maize ... O. T. Bonnett	269–287
A Comparative Developmental Study of a Dwarf Mutant in Maize, and Its Bearing on the Interpretation of Tassel and Ear Structure ... S. G. Stephens	289–299

	PAGE
Studies on the Structure of the Maize Plant .... Hugh C. Cutler and Marian C. Cutler	301–316
Right-Handed and Left-Handed Corn Embryos .... Paul Weatherwax	317–321
A Morphological Analysis of Row Number in Maize .... Edgar Anderson and William L. Brown	323–336
The Vascular Anatomy of the Four-rowed Ear of Corn .... R. A. Laubengayer	337–340
General Features of the Epidermis in *Zea Mays* .... Henri Prat	341–351
Comparative Histology of the Female Inflorescence of *Zea Mays* L. .... Lee Wayne Lenz	353–376
The Role of Pod Corn in the Origin and Evolution of Maize .... Paul C. Mangelsdorf	377–404
General Index to Volume XXXV	405–408

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FLORA OF PANAMA

Part V. Fascicle 1

LAURACEAE

CAROLINE K. ALLEN

Evergreen trees or shrubs in the Panamanian species, rarely herbs *(Cassytha)*; leaves alternate, occasionally subverticillate, rarely opposite, entire, penninerved, triplinerved or subtriplinerved, rarely subquintuplinerved. Inflorescence axillary or subterminal, usually paniculate. Flowers usually perfect, rarely dioecious, perianth 6-lobed, fertile stamens usually 9, in series of three; anthers erect, 2- or 4-celled, those of the two outer series usually introrse, those of the inner extrorse or occasionally the third of the inner series only fertile; filaments of the inner series always biglandular; staminodia, representing a fourth series, may be present or absent. Ovary superior, 1-celled, bearing a style, usually well developed, and a variable stigma. Fruit a 1-seeded berry, subtended by a disk or cupule formed by the enlarged perianth-tube, sometimes crowned by the remnants of the perianth-lobes, and supported by the usually enlarged pedicel.

About 50 genera throughout the world, one of the heaviest areas of concentration being in the Malaysian region and Eastern Asia, the second focus being in tropical America. A few genera only are to be found in Africa and one in Europe. Of those genera occurring in Central and South America, three are also abundant in Eastern Asia and Malaysia, namely, *Beilschmiedia, Cryptocarya* and *Phoebe*. More rare for the Lauraceae is the distribution noted in the genera *Lindera* and *Sassafras,* where a single rather widespread species of each occurs in the United States, the remaining species of *Sassafras* occurring in Eastern Asia, and of *Lindera* in Eastern Asia and Malaysia. *Litsea* and *Persea* occur in the United States, along the Atlantic Coast, and from upper Mexico into South America.

The following is based on the publication by the author, 'Studies in the Lauraceae, VI, Preliminary Survey of the Mexican and Central American Species' (Jour. Arnold Arb. 26:280–434. 1945), where a more complete synonymy is available. In the present treatment of the family fairly broad descriptions of the genera are given unless otherwise indicated. Data on the commercial uses of the woods are obtained from field notes and in some cases from 'Timbers of the New World,' by Record & Hess.

Issued March 22, 1948.

a. Anthers 4-celled.
  b. Staminodia large, cordate, stipitate.
    c. Perianth-lobes usually unequal or at most subequal; usually the lower cells of the anther touching the upper at their sides.............. 1. Persea
    cc. Perianth-lobes equal or subequal; usually lower cells of the anther touching the upper at their bases.............. 2. Phoebe
  bb. Staminodia small, inconspicuous or occasionally lacking.
    c. Flowers perfect or dioecious; perianth-lobes not reflexed at anthesis, thin in texture; cells of the anthers arranged in two planes, one above the other.............. 3. Ocotea
    cc. Flowers always perfect; perianth-lobes usually fleshy, papillose and reflexed at anthesis; cells of the anthers arranged in an arc.............. 4. Nectandra
aa. Anthers 2-celled.
  b. Flowers perfect.
    c. Flowers with 9 fertile stamens; fruit subtended by cupule with single margin or subtended by a naked pedicel.
      d. Staminodia well developed; fruit subtended by naked pedicel..... 5. Beilschmiedia
      dd. Staminodia absent; fruit subtended by dentate cupule.............. 6. Aiouea
    cc. Flowers with 3 fertile stamens; fruits subtended by cupules with double or triple margins.............. 8. Licaria
  bb. Flowers dioecious.............. 7. Endlicheria

The genus *Cassytha* probably is represented in Panama by *C. filiformis* L. which is found in the tropics of the entire world, but is not common in Central America. The plants are parasitic herbs, similar in habit and general appearance to *Cuscuta*, but the floral structure is typically lauraceous.

Exotic Lauraceae cultivated in Panama include *Cinnamomum Camphora* (L.) Nees & Eberm., the source of commercial camphor *(Alcanfor)*, and *C. zeylanicum* Nees, cinnamon *(Canela)*.

1. PERSEA Miller

Persea Miller, Gard. Dict. ed. 8. 1768.

Evergreen trees (in Panama). Leaves alternate or subverticillate, the blades penninerved. Inflorescence usually of numerous axillary or subterminal panicles, frequently subsessile (in Panama), pubescent, with persistent or deciduous bracts, often many-flowered. Flowers perfect, usually fairly conspicuous, sessile or pedunculate. Perianth-tube none, or so shallow as to appear lacking. Perianth-lobes often spreading, frequently conspicuously unequal, pubescent, usually persistent. Stamens of all three series fertile (in Panama), with pubescent filaments; anthers 4-celled (in Panama), the cells in 2 planes, the bases of the 2 upper cells laterally tangential to the apices of the 2 lower cells; cells of the two outer series introrse, the filaments long and sometimes pubescent; those of the inner series extrorse or the 2 upper cells may be lateral and the 2 lower extrorse, with the filaments distinctly biglandular. Staminodia usually large, conspicuous, subcordate and pubescent, with the stipes of varying length, or occasionally ligulate. Ovary subglobose or ovoid, pubescent or glabrous, sometimes constricted at the base or slightly stipitate. Style usually filiform, usually longer than the ovary, and occasionally pubescent. Stigma inconspicuous, discoid or conspicuous and triangularly peltate. Fruit small, globose or large, fleshy, pear-shaped, edible, usually glabrous, entirely or almost entirely exserted at maturity, and subtended by persistent or occasionally deciduous perianth-lobes.

The genus consists of approximately 145 species. The largest number is native to South America (70), with the heaviest concentration in Brazil. Twenty-two species occur in Mexico and Central America. Of these, five at the most are common to both regions. Thirteen are to be found in the West Indies and eight in the United States. Twenty Asiatic species are known with ten from Malaysia and one each from Australia and the Mascarenes. Two species are reported from the Azores and Canary Islands, but these perhaps should not be included in the genus. Except for the Avocado, the genus is unimportant commercially.

a. Leaf-blades coriaceous, 10–30 × (3–) 10–15 (–20) cm., elliptic, irregularly or obovate-elliptic, ovate, or obovate.
  b. Blades irregularly or obovate-elliptic, ovate or obovate, coriaceous, 15 (–20) cm. broad, pubescent to glabrous or glaucous beneath; petioles 1.5–5 cm. long; panicles usually numerous in axils of persistent upper leaves; ovary pubescent; large edible fruit.
    c. Branchlets yellow-tomentellous becoming glabrous or subglabrous; blades variable, usually elliptic, lower surface subglaucous, usually up to 20 cm. broad, acuminate; floral bracts deciduous; fruit variable.......... 1. P. AMERICANA
    cc. Branchlets and lower surface of leaf-blades densely brown-tomentose; blades 10–15 cm. broad, obtuse or abruptly acuminate; floral bracts persistent; fruit obovoid.......... 2. P. SCHIEDEANA
  bb. Blades always elliptic, rigidly coriaceous, usually not more than 7–8 cm. broad, occasionally 12 cm., glabrous; petioles not more than 1.5 cm. long; numerous panicles in axils of deciduous upper leaves; ovary glabrous.......... 3. P. RIGENS
aa. Leaf-blades pergamentaceous or chartaceous, up to 17 × 7.5 cm., always elliptic.
  b. Outer perianth-lobes small and scale-like, approximately one-fourth the length of the inner; fruit shining, 7 mm. in diameter.......... 4. P. SKUTCHII
  bb. Outer perianth-lobes more than one-half the length of the inner; fruit with bluish bloom, 10–11 cm. in diameter.......... 5. P. VERAGUASENSIS

1. PERSEA AMERICANA Miller, Gard. Dict. ed. 8. 1768.

Tree to 20 m. high; branches light gray, fissured. Leaves crowded at branchlet tips; petioles yellow or yellow-green, pubescent to glabrous, 1.5–5 cm. long; blades pubescent to glabrous, dark green, somewhat shining above, glaucous below, coriaceous, ovate or obovate-oblong, 10–30 cm. long and 3–20 cm. broad, the base cuneate or obtuse, the apex acute or obtuse or obtusely acuminate, the lateral nerves up to 10 pairs, elevated beneath, the venation yellow. Inflorescence of axillary subterminal panicles, densely pubescent, many-flowered, with deciduous bracts. Flowers small (6–7 mm. long, 0.5–1.5 mm. in diameter), fragrant, tomentose, with yellow-green pedicels up to 5 mm. long; perianth yellow-green or light yellow, the lobes unequal, the outer 3 mm. long, the inner 6 mm. long, persistent; stamens of ser. I & II 2.5–3.5 mm. long, those of ser. III longer, with extrorse anthers; staminodia short-stiped; gynaecium 4–5.5 mm. long, the ovary pubescent, the stigma discoid. Fruit large, pear-shaped, globose, or oval, 7–20 × 7–10 cm., the pulp fleshy, thick, juicy, oily, the seed large, 2.5–5 cm. in diameter, globose.

Native probably of Mexico and Central America, and possibly the West Indies; for centuries widely cultivated for its edible fruit throughout these regions and all tropical and subtropical countries. Known as *Aguacate, Avocado* and "Alli-

gator Pear." Seeds yield proprietary oil. Wood medium to coarse in texture, easily worked but not durable and therefore commercially unimportant.

2. PERSEA SCHIEDEANA Nees, Syst. Laurin. 130. 1836.

Tree (or shrub) 20–50 m. high; branchlets brown-tomentose becoming glabrescent; petioles up to 3 cm. long; blades shining above, glaucescent and brown-tomentose beneath, irregularly elliptic, often obovate-elliptic, 24–30 cm. long and up to 15 cm. broad, the base usually rounded, frequently almost truncate, the apex rounded, acute or abruptly acuminate or obtuse, lateral nerves 8–10 pairs, the

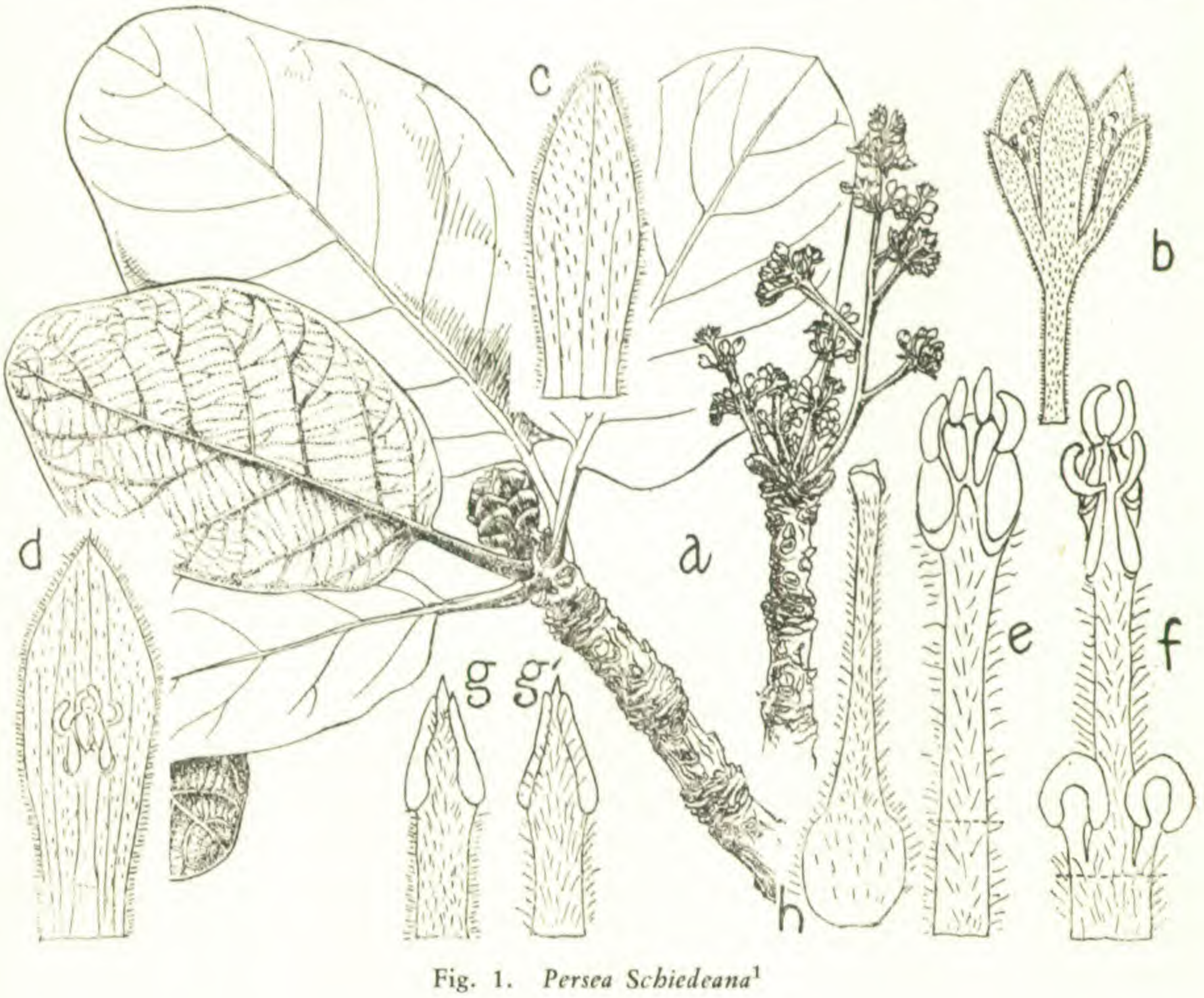

Fig. 1. *Persea Schiedeana*[1]

lowermost diverging from the costa at an angle of 75–80°, the upper 35–40°, loosely reticulate. Inflorescence of numerous subterminal subsessile panicles 10–15 cm. long, with persistent bracts. Flowers 6–8 mm. long, borne on slender pedicels usually of equal length; perianth pale greenish yellow, turning crimson at the base or light rose with age, the lobes subequal, to 7 mm. long, persistent, pubescent without, stamens to 3.8 mm. long, the filaments twice the length of the anthers, the two upper cells often only one-half the size of the two lower; those of ser. III with conspicuous, cordate, stipitate glands; staminodia to 2.5 mm. long, cordate,

[1] In this and the following Lauraceae illustrations the habit sketches (*a*) are approx. × ⅔; flower (*b*), approx × 3; outer and inner perianth-lobes (*c* and *d*), approx. × 7; stamen (ser. I & II, *e*, and ser. III, *f*), × approx. 13; staminodium (*g*), × approx. 13; gynaecium (*h*), × approx. 13. Habit sketches drawn by Mrs. Martha Suttis Koteles.

stipitate, the pubescent stipe one-half the entire length; gynaecium ±3.8 mm. long, the ovoid ovary pubescent, the slender style pubescent, twice the length of the ovary, the stigma inconspicuous. Fruit similar to that of *P. americana,* obovoid, early very pubescent, later becoming glabrescent and roughened, subtended by thickened, persistent perianth-lobes which are borne on enlarged pedicels, both lobes and pedicels becoming glabrescent.

Native of Mexico and Central America; cultivated particularly in Guatemala for its edible fruit. Utilized to a limited extent locally for interior construction, but is not resistant to insects and hence is of little economic value. Native name *Aguacatón;* known commercially as "Guatemala Avocado."

CHIRIQUÍ: vicinity of Cerro Punta, *Allen 1534;* Bajo Chorro, Boquete, *Davidson 304, 427, Pittier 3132.* PANAMÁ: Isla Taboga, *Allen 1288.*

Fig. 2. *Persea rigens*

3. PERSEA RIGENS C. K. Allen in Jour. Arnold Arb. 26:297, 432. 1945.

Tree to 30 m. high; branchlets stout, glabrous, brown or maculate-brown. Leaves alternate or subverticillate; petioles brown, glabrous, thick, scarcely canaliculate, up to 1.5 cm. long; blades glabrous, castaneous or olive-green, membranaceous becoming rigidly coriaceous, elliptic, (12–) 20–25 (–35) cm. long and 7 (–12) cm. broad, the base cuneate, the apex obtuse or obtusely subacuminate, the lateral nerves 7–9 pairs, diverging arcuately at an angle of 45–55° from the costa, the venation conspicuous, conspicuously elevated beneath, the minute

reticulation prominent. Inflorescence of numerous panicles in axils of deciduous upper leaves, densely greenish-fulvous-whitish-pubescent, up to 10 cm. long, the peduncle 6 cm. long. Flowers tomentose, to 4 mm. long, with pedicels of equal length; perianth campanulate, the subequal lobes thick, up to 3 mm. long; stamens of ser. I & II often subpetaloid, up to 2.15 mm. long, those of ser. III with stiped glands; staminodia to 1.7 mm. long, subcordate, stipitate; gynaecium glabrous, to 2.8 mm. long, the ovary ovoid or subglobose, equal to or twice the length of the somewhat robust style, the stigma subtriangular, conspicuous. Fruit unknown, the subtending pedicel thickened and rough, up to 7 mm. long, bearing the expanded remnants of the perianth-lobes.

Native of Panama. Known as "Timber Sweetwood," *Pizarrá*. Wood used for boards and rough lumber.

BOCAS DEL TORO: Daytonia Farm, region of Almirante, *Cooper 458 (Y12076)*. CHIRIQUÍ: near sawmill on Río Chiriquí Viejo, 3 km. n. of Camp El Volcán, *Little 6057, 6058, 6075*.

Easily distinguished by the dense many-panicled inflorescences heavily grayish- or fulvous-white-tomentose.

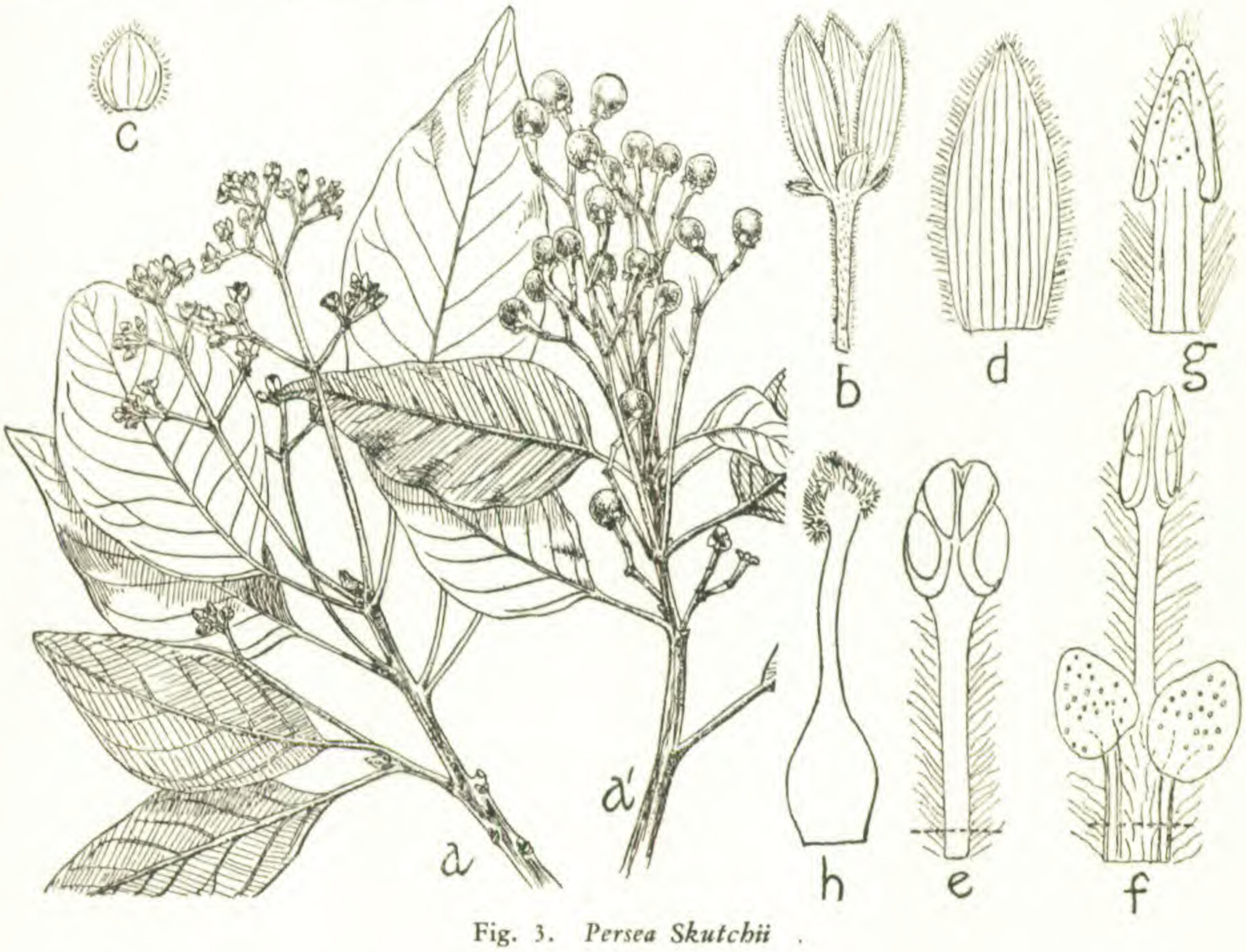

Fig. 3. *Persea Skutchii*

4. Persea Skutchii C. K. Allen in Jour. Arnold Arb. 26:298. 1945.

Spreading tree to 25 m. high; branchlets reddish, striate, pale appressed-ferruginous-tomentose becoming glabrous. Leaves alternate or subverticillate; petioles brown, slender, scarcely canaliculate, up to 3.5 cm. long; blades glabrous and pale green above, sparsely pubescent and pale brown or glabrous beneath, pergamenta-

ceous, elliptic, 10–14 (–17) cm. long and 5 (–7.5) cm. broad, the base rounded or cuneate, often oblique, the apex obtuse, acute, or acuminate, often emarginate, the margin undulate, the lateral nerves up to 12 pairs, diverging from the costa at an angle of 55 (–65°). Inflorescence of loose, axillary, fulvous-sericeous panicles up to 12 cm. long. Flowers to 6 mm. long, with slender pubescent pedicels nearly as long; perianth campanulate, pale yellow, lobes unequal, the outer 1.5 mm. long, the inner 5 mm. long; stamens of ser. I & II to 3.36 mm. long, the filaments almost twice the length of the anthers, the stamens of ser. III slightly longer, with stipitate glands; staminodia conspicuous, pubescent, subcordate, to 2.7 mm. long, stipitate; gynaecium glabrous, 3.42 mm. long, the ovary ovoid, slightly constricted at the base, shorter than the style, the stigma conspicuously triangular-peltate. Fruit black, shining, glabrous, globose, inconspicuously apiculate, about 7 mm. in diameter, the pedicel sparsely pubescent, somewhat thickened at the apex to nearly 2 mm. in diameter, and crowned with the remnants of the more or less reflexed perianth-lobes measuring about 6 mm. in diameter.

Native to Costa Rica and Panama from 300 to 1675 meters altitude.

COCLÉ: vicinity of El Valle, south rim (dry), *Allen 1781;* hills south of El Valle de Antón, *Allen 2498.*

Near *Persea caerulea* from South America, but may be distinguished by inflorescences that are shorter than the leaves, which are acute or subacuminate, with less erect lateral nerves, and by the blackish depressed-globose fruits not more than 8 mm. in diameter, with no conspicuous bloom.

5. PERSEA VERAGUASENSIS Seemann, Bot. Voy. Herald, 193. 1854.

Tree from 3–18 (–25) m. high; branchlets densely striate, angled, densely subferruginous-sericeous becoming glabrescent and atro-rubescent or gray-brown-maculate. Leaves alternate; petioles slender to robust, rusty-pubescent to glabrescent, 2.5–3 cm. long; blades dark green, shining above, glabrescent and pale or glaucescent beneath, and sericeous-pubescent, chartaceous, oblong-elliptic or elliptic, 8–17 cm. long and up to 6 cm. broad, the base obtuse or cuneate, sometimes subrhomboid, the apex acute, acuminate or obtuse, the lateral nerves 8–10 pairs, conspicuous beneath, diverging from the costa at an angle of 35–45°. Inflorescence axillary, of few-flowered, ferruginous- or buff-sericeous-tomentose panicles shorter than the leaves, up to 6 cm. long, the peduncle sericeous. Flowers to 4 mm. long, sessile or with sericeous pedicels up to 1 mm. long; perianth-lobes fleshy, unequal, the outer 1.3–2.5 mm. long, the inner 2.5–4.5 mm. long; stamens 2.15–2.6 mm. or more long (ser. II & III longer); staminodia to 1.7 mm. long, ligulate, pubescent; gynaecium 3.42 mm. long, the ovary glabrous, ovoid, slightly stipitate, the style pubescent, the stigma triangular-discoid. Fruit globose, apiculate with bluish bloom, 10–11 mm. in diameter, subtended by the enlarged perianth-lobes and seated on the enlarged red pedicel.

Woods of Costa Rica south into Panama from an altitude of 600 to 2300 meters. Described by Seemann from Volcán de Chiriquí.

Fig. 4. *Persea veraguasensis*

CHIRIQUÍ: Bajo Mona, Boquete, *Davidson 516;* savannas of Boquete, *Davidson 753;* Río Chiriquí Viejo Valley near El Volcán, *P. White 213;* in the open llanos about a mile from Bambito, valley of the upper Río Chiriquí Viejo, *P. White 334.*

Also similar to *Persea caerulea* from South America, but easily separated by the few-flowered panicles shorter than the leaves, the shorter leaf-blades with nerves, and petioles that are not reddish in color.

2. PHOEBE Nees

PHOEBE Nees, Syst. Laurin. 98. 1836.

Evergreen trees or shrubs. Leaves alternate, the blades triplinerved or subtriplinerved, occasionally penninerved. Inflorescence paniculate, axillary and usually subterminal; panicles loose or narrow, strict, somewhat racemose, with no involucre. Flowers perfect, pedicellate or occasionally sessile. Perianth-tube short although usually well-defined. Perianth-lobes approximately equal or subequal, occasionally the three outer lobes shorter, usually incurved, rarely reflexed, and, for the most part in Panama, thin in texture. Stamens of all three series with four fertile anther-cells; anther-cells of the two outer series introrse, the two upper cells slightly smaller than the two lower, frequently with inconspicuous connective tissue; two lower anther-cells of inner series extrorse, the two upper usually slightly smaller, lateral or at most laterally extrorse; filaments of inner series conspicuously biglandular. Staminodia well developed, conspicuous, cordate, stipitate,

the stipe usually pubescent. Ovary glabrous, usually ellipsoid, occasionally subglobose. Style cylindrical, slender, equal to or shorter than the ovary, glabrous. Stigma usually triangularly discoid or capitate, fairly conspicuous. Fruit a berry, borne in a shallow somewhat fleshy cupule frequently crowned by the remnants of the perianth-lobes, and subtended by the enlarged pedicel.

The genus consists of approximately 120 recognized species, about 80 of which are in this hemisphere. Of this number one-half occur in Mexico and Central America, the bulk of the remainder in South America with about a half-dozen in the West Indies. In the eastern hemisphere the species are to be found about equally divided between Malaysia and the mainland of Asia. Only one species from Brazil is important commercially, being used for interior construction and furniture.

a. Leaf-blades triplinerved or subtriplinerved.
  b. Blades not more than 10 cm. long........ 1. P. BRENESII
  bb. Blades usually not less than 12 cm. long.
    c. Blades definitely triplinerved, coriaceous; nervation not pale reddish; panicles 10–19 cm. long.
      d. Blades narrowly elliptic; inflorescences loose, spreading, few-flowered panicles........ 2. P. COSTARICANA
      dd. Blades elliptic to lanceolate or oblong-elliptic; inflorescences numerous, narrowly racemose, many-flowered panicles........ 3. P. MEXICANA
    cc. Blades subtriplinerved, membranaceous becoming pergamentaceous; nervation pale reddish; panicles not more than 12 cm. long........ 4. P. JOHNSTONII
aa. Leaf-blades penninerved........ 5. P. PITTIERI

1. PHOEBE BRENESII Standley in Field Mus. Publ. Bot. 18:459. 1937.

Small tree 5–6 (occasionally 4–22) m. high; branchlets slender, early fulvous-tomentellous becoming glabrescent, striate and even angled. Leaves alternate or subopposite occasionally; petioles slender, pubescent becoming glabrous, canaliculate, up to 2 cm. long; blades early glabrous above except for remnant of pubescence on venation, glabrescent beneath except for axillary glands, membranaceous becoming coriaceous, elliptic or oblong-elliptic, rarely broadly elliptic, 3.5–7 (–10) cm. long, 2–3.5 (–4.5) cm. broad, the base cuneate, the apex abruptly acuminate or caudate-acuminate, triplinerved, the slender lowermost pair of nerves less obscure than the 2 or 3 upper pairs, and diverging from the costa at about 0.5–1 cm. above the base. Inflorescence axillary and subterminal, loosely paniculate, glabrous or glabrescent, up to 12 cm., usually shorter than the leaves, the slender peduncles glabrous, up to 7 cm. long. Flowers 3.4 mm. long, glabrous, the pedicels of equal length; perianth-lobes 2.5 mm. long, ovate, thin, pubescent within; stamens of ser. I & II 1.7 (–2.15) mm. long, frequently somewhat emarginate, the oblong anthers usually equaling or sometimes nearly twice the length of the slender pubescent filaments, the stamens of ser. III 2.15 mm. long, the more narrow anthers equalling the biglandular filaments, glands conspicuous, cordate, stipitate; staminodia cordate, stipitate, 1.4 mm. long, the pubescent stipe broad, more than one-half the entire length; gynaecium glabrous, 2.4 mm. long, the ovary subglobose, shorter than the slender style, the stigma triangularly discoid.

Fig. 5. *Phoebe Brenesii*

Fruit oblong-ellipsoid, 15 × 5 cm., the subtending cupule shallow, to 5 mm. long and broad, and 2 mm. deep, crowned by the remnants of the partially deciduous perianth-lobes, the pedicel thickened and up to 5 mm. long, expanding slightly towards the apex.

Central Costa Rica at 600 to 1000 meters altitude, and in Panama up to 1140 meters.

CHIRIQUÍ: Boquete, *Davidson 641;* Bajo Mona, Robalo Trail, western slope of Cerro Horqueta, *Allen 4832.*

Resembles *Phoebe mexicana* and *P. costaricana,* but is readily separated from the former by its loose spreading inflorescence, and from the latter by its smaller leaves, and shorter, less densely flowered inflorescence.

2. PHOEBE COSTARICANA Mez & Pittier ex Mez in Bull. Herb. Boiss. II. 3:230. 1903.

Small tree 8–20 m. high; branchlets reddish chestnut, somewhat maculate, definitely angled, appressed fulvous-pubescent becoming glabrous. Leaves alternate; petioles fairly stout, glabrous, canaliculate, 7–12 (–20) mm. long; blades glabrous throughout except for glands on the lower surface, coriaceous, narrowly elliptic, 10–12 (–15) cm. long and 2.5–3.5 (–6) cm. broad, the base cuneate, the apex subacuminate or acute, triplinerved, the costa impressed above and more

Fig. 6. *Phoebe costaricana*

prominent throughout than the slender lateral nerves, of which the lowermost pair diverge 1–1.5 cm. from the base at an angle of about 35°, persisting well past the middle of the blade, the inconspicuous upper pairs diverging at an angle of about 55°; pubescent axillary glands present in the axils of the lowermost pair of nerves. Inflorescence axillary and subterminal, panicles longer than the leaves, slender, broad and spreading, glabrous, few- to many-flowered, 12–19 cm. long, the peduncle 6–10 cm. long. Flowers 3–4 mm. long, the pedicels 4–5 mm. long; perianth subcampanulate, yellow or greenish white, the lobes subequal, 1.9–2.15 mm. long, ovate or ovate-elliptic, membranaceous, pubescent; stamens of ser. I & II 1.7 mm. long, the ovate anthers equaling the filaments, the stamens of ser. III to 2.15 mm. long, the oblong anthers biglandular, the glands subsessile, conspicuous, cordate; staminodia cordate, stipitate, to 1 mm. long; gynaecium glabrous, to 2.5 mm. long, the ovary ellipsoid or ellipsoid-ovoid, about equaling the slender style, the stigma triangular and not too conspicuous. Fruit ellipsoid, apiculate, 2 × 1 cm., the subtending cupule sometimes suburceolate, 9 mm. long, 8–12 mm. in diameter and 3 mm. deep, crowned by the persistent thickened perianth-lobes, supported by the enlarged, comparatively slender pedicel.

Native of Costa Rica and adjacent Panama, at an altitude of 1000 to 1700 meters, on forested hills. Known as *Sigua*.

CHIRIQUÍ: Bajo Mona, Boquete, *Davidson 583*; forests around Boquete, *Pittier 2998, 3146*; Finca Lérida to Boquete, *Woodson, Allen & Seibert 1099*; vicinity of Boquete, east of Río Caldera, *Allen 4657*.

Most nearly related to *Phoebe effusa*, a native of Mexico, from which it may be distinguished by differences in leaf-structure. The blades of *P. costaricana* are more attenuately cuneate; there are usually only four pairs of lateral nerves, the lowermost pair often being extremely conspicuous and bearing pubescent glands in the axils; the petioles are usually stout, glabrous or glabrescent and up to 1.5 cm. long, and the pedicels usually equal the perianth, rarely exceed it in length.

Fig. 7. *Phoebe mexicana*

3. PHOEBE MEXICANA Meissner in DC. Prodr. 15^1:31. 1864.

Small tree to 12 m. high; branchlets reddish black or reddish brown, sulcate becoming striate, grayish fulvous-pubescent becoming glabrescent at maturity. Leaves alternate; petioles stout, glabrescent becoming glabrous, canaliculate, to 2 (–2.5) cm. long; blades variously pubescent, usually glabrous above, often glabrous beneath except for the glands, coriaceous, elliptic, lanceolate- or oblong-elliptic, 15 (–26) cm. long and 5 (–10) cm. broad, the base cuneate or somewhat obtuse or rounded, the apex subacute or acuminate to caudate-acuminate, tripli-nerved, the costa prominently impressed above and elevated beneath, lateral nerves up to 7 pairs, slender and very obscure, the more prominent lowermost pair with usually prominent pubescent glands in their axils and diverging from the costa at an angle of about 25°, the upper pairs at an angle of about 55°. Inflorescence

of numerous axillary and subterminal, racemose panicles, pubescent becoming glabrescent, many-flowered, reddish, 10–15 cm. long, the peduncles usually 2–4 (–5) cm. long. Flowers fulvous-pubescent, small, 3–4 mm. long, sessile or with the pedicels 2 (–3) cm. long; perianth campanulate, white, the lobes thin, ovate, the three outer to 2 mm. long, the three inner to 3 mm. long; stamens of ser. I & II to 1.7 mm. long, the elliptic anthers equaling the slender filaments, the stamens of ser. III to 2.15 mm. long, the filaments biglandular, the glands subreniform, stipitate, about one-third the length of the entire stamen; staminodia narrowly cordate, stipitate, approximately 1 mm. long, the stipe slender, pubescent, slightly more than one-half the entire length; gynaecium glabrous, 2.5 mm. long, the ovary broadly ellipsoid to obovoid, less than one-half the length of the slender style, the stigma conspicuous, slightly dilated, discoid, or deltoid. Fruit slightly obovoid, apiculate, about 1 cm. long and 7 mm. broad, the subtending cupule campanulate, 5 mm. long, 7 mm. in diameter and 2 mm. deep, bearing the brittle remains of the persistent perianth-lobes, the pedicel being enlarged to about 5 mm. in length.

Found generally throughout southwestern Mexico and Central America, at varying altitudes from 15 meters along the coast to 2800 meters in the mountains of Guatemala.

CANAL ZONE: near Culebra, *Pittier 3438;* hospital grounds at Ancon, *Pittier 3957.*

Distinct because of the numerous strict raceme-like panicles with short branchlets, borne so close to the main axis as to give a spike-like appearance. In the specimens from Panama, the leaf-blades are more coriaceous, shorter, more definitely elliptic, and more blunt at the apex. In all other respects, however, the Panamanian trees resemble those growing farther north.

4. PHOEBE JOHNSTONII C. K. Allen in Jour. Arnold Arb. 26:433. 1945.

Small, often bushy aromatic trees to 15 m. high; branchlets reddish, striate, gray-sericeous becoming at length glabrous. Leaves alternate; petioles reddish, pubescent becoming glabrous, slender, canaliculate, up to 1.5 cm. long; blades glabrous above and beneath except for the nerves and axillary glands, shining and olive-green above, pale beneath, in the young stages membranaceous becoming pergamentaceous, lanceolate-elliptic, 8–14 cm. long and 2.5–4.5 cm. broad, the extreme base narrowly cuneate or attenuately cuneate throughout, the apex obtusely and attenuately acuminate or subcaudate-acuminate, subtriplinerved, the nervation pale reddish, the lateral nerves, of which there are 4 or 5 pairs, slender, the lowermost pair diverging from the costa at an angle of 25–35°, and more conspicuous than the upper pairs which diverge at an angle of 45°; axillary glands of the lowermost pair of nerves less obscure than those of upper pairs. Inflorescences axillary and subterminal, numerous, racemose or rarely broad panicles up to 12 cm. long, early yellow-white becoming reddish, the peduncle to 2 (–3) cm. long, striate, pubescent becoming glabrescent. Flowers to 4 mm. long, the pedicels to 3 mm. long; perianth subcampanulate, pale yellow, lobes subequal, ±2.4–3

Fig. 8. *Phoebe Johnstonii*

mm. long, ovate, elliptic or elliptic-lanceolate, membranaceous, pubescent; stamens of ser. I & II ± 1.7 mm. long, the ovate anthers equaling the filaments, the stamens of ser. III ± 2 mm. long, the subovate anthers emarginate and biglandular, the glands subsessile, conspicuous, reniform; staminodia ovate, subcordate, stipitate, to 1.15 mm. long; gynaecium glabrous, ± 2.5 mm. or more long, the ovary ovoid or subglobose, almost equaling the slender style, the stigma subcapitate, somewhat conspicuous. Fruit green, glabrous, ellipsoid, minutely apiculate, 1 cm. × 7 mm., the subtending cupule 5 mm. long, 7 mm. in diameter and 4 mm. deep, crowned by the persistent, slightly thickened, reddish perianth-lobes, supported by the thickened, reddish pedicel up to 6 mm. long.

Native to Panama at low altitudes, although collected on the mainland only on the hospital grounds at Ancon, Canal Zone, and to San José Island of the Perlas Archipelago, where it occurs abundantly according to the collector.

CANAL ZONE: hospital grounds at Ancon, *Pittier 2750*. PANAMÁ: San José Island, Perlas Archipelago, Gulf of Panama, *Johnston 505, 512, 553, 583, 666, 667, 697, 713, 773;* WITHOUT LOCALITY: *Hayes 1017, 1018.*

Similar to *Phoebe mexicana* found throughout Mexico and Central America, and to *P. Ehrenbergii* of Mexico, but easily separated from the former by the shorter panicles bearing flowers that are never whitish gray-pubescent, and by leaf-blades that are thinner in texture and on the whole more narrow. From the latter it may be separated by the many-flowered inflorescences, usually not more than 8 cm. long, with flowers not more than 4 mm. long and never pruinose.

Fig. 9. *Phoebe Pittieri*

5. PHOEBE PITTIERI Mez in Bot. Jahrb. 30, Beibl. 67:16. 1901.

Small tree or shrub 3–5 m. high; branchlets fulvous- or yellowish-tomentose, somewhat sericeous in the very young stages, becoming fuscous and harsh to the touch. Leaves alternate or subopposite, near the apex of the branchlet; petioles pubescent, shallowly canaliculate, up to 1 cm. long; blades glabrous and almost shining above except for the pubescent venation, roughly pubescent beneath, subcoriaceous or pergamentaceous, lanceolate or elliptic, 7 (–9) cm. long and 2.5–3 cm. broad, the base cuneate, the apex acuminate to obtusely acute, penninerved, the nervation conspicuously pubescent beneath, the costa slightly elevated and pubescent above and prominently so beneath, the lateral nerves usually 5 pairs, slender and obscure above and prominently elevated beneath, diverging from the costa at an angle of 35–45°, with inconspicuous axillary glands, reticulation obscure above, more prominent beneath. Inflorescence axillary, panicles pubescent becoming glabrescent, purplish, few-flowered, not more than 5.5 (–7) cm. long, the peduncles up to 2 (–4) cm. long. Flowers up to 5 mm. long, the slender filamentous pedicels up to 8 mm. long; perianth spreading campanulate, white (purplish in the dried state), the lobes subequal, 3 mm. long, thick, papillose, elliptic, often reflexed; stamens of ser. I & II 1.7 mm. long, the roundish or ovate anthers equaling or longer than the filaments, the stamens of ser. III approximately equal in length to or longer than the outer series, the oblong or square anthers equaling the biglandular filaments, the glands large, sessile or only slightly stipitate; staminodia broadly ovate, subcordate, stipitate, 1–1.5 mm. long, the stipe

broad and spreading at the apex, pubescent two-thirds the entire length; gynaecium glabrous, 2.8 mm. long, the ovary somewhat obovoid or occasionally subglobose, longer than the style, the stigma rather inconspicuous, discoid, deltoid. Fruit greenish to purple, ellipsoid, 12–15 × 9–11 mm., the subtending cupule flaring, undulate, fluted, cyathiform, reddish, 5 mm. long, 9 mm. in diameter and 3 mm. deep, the enlarged pedicel up to 1 cm. long and expanded to 4 mm. in diameter at the apex.

Woods of Costa Rica and Panama, at an altitude of 1050 to 2200 meters, usually in moist woods; cloud forests of San Salvador, at an altitude of 2000–2150 meters.

CHIRIQUÍ: cloud- and rain-forests of Cerro Horqueta, *von Hagen & von Hagen 2031, 2070.*

Most outstanding for the penninerved leaves which are clothed with a rough pubescence harsh to the touch, and the branchlets which are early sericeous, becoming fulvous- or yellowish-tomentose and finally fuscous.

3. OCOTEA Aublet

OCOTEA Aublet, Pl. Guian. 2:780, *t. 310.* 1775.

Oreodaphne Nees, Pl. Laurin. 15. 1833.
Dendrodaphne Beurling in Vet. Akad. Handl. Stockholm 1854:145. 1856.
Sassafridium Meissner in DC. Prodr. 15^1:171. 1864.

Evergreen trees or shrubs. Leaves usually alternate, occasionally subverticillate or subopposite, the blades penninerved. Inflorescence generally axillary or subterminal, paniculate. Flowers usually perfect, occasionally dioecious, usually distinctly pedicellate. Perianth-tube conspicuous or lacking entirely. Perianth-lobes equal or at most subequal, thin and membranaceous to thick, fleshy and papillose, mostly deciduous. Two outer series of stamens in the perfect flowers variously shaped with filaments of varying lengths; anthers with or without connective tissue, with 4 introrse cells arranged in 2 planes, one above the other. Inner series of stamens with longer filaments bearing 2 sessile or stipitate glands varying in size and shape; anthers with 4 cells extrorse, or the 2 upper lateral and the 2 lower extrorse. Staminodia, if present, usually aborted. Gynaecium usually entirely glabrous, the style rarely pubescent. Stigma usually conspicuously triangular and often decurrent, occasionally inconspicuous and somewhat discoid. First three series of stamens of dioecious pistillate flowers replaced by staminodia with variously developed anthers; gynaecium as in perfect flowers. Stamens of staminate flowers well developed; gynaecium absent or aborted. Fruit a berry borne in a usually simple-margined cupule that is flat and disk-like or campanulate to hemispherical, with an undulate margin supported by an enlarged pedicel.

A genus consisting of approximately 340 recognized species centered, except for 27 or so which occur in Madagascar and the Mascarene Islands, in tropical America. About 21 of the American species are to be found in the West Indies,

5 in Mexico, 29 in Central America, and the remaining in South America, the South American ones being native to Brazil. Further study may show the Madagascar and Mascarene species to belong to another genus. Used for furniture, interior construction, and one species for marine construction because of durability of the timber.

a. Largest leaf-blades not less than 20 cm. long.
  b. Leaf-blades heavily coriaceous, and densely and conspicuously reticulate and shining above.
    c. Leaf-blades pubescent beneath; petioles pubescent .... 1. O. Cooperi
    cc. Leaf-blades glabrous beneath; petioles glabrous.
      d. Leaf-blades elliptic, prominently shining above, base cuneate, 6 (–9) pairs lateral nerves .... 2. O. Seibertii
      dd. Leaf-blades elliptic to subobovate, somewhat shining above, the base attenuate, 12 or more pairs lateral nerves .... 3. O. glomerata
  bb. Leaf-blades variable in texture, and, if densely reticulate, not conspicuously so and not shining above.
    c. Leaf-blades conspicuously ferruginous- or subferruginous-tomentose beneath; venation conspicuously pubescent; inflorescence densely ferruginous- or subferruginous-tomentose .... 4. O. palmana
    cc. Leaf-blades glabrous or glabrescent beneath, not conspicuously ferruginous- or subferruginous- or brownish-tomentose.
      d. Leaf-blades definitely obovate.
        e. Base of leaf-blades decurrent, sometimes very conspicuously so, and recurved .... 5. O. Ira
        ee. Base of leaf-blades never conspicuously decurrent or recurved.. 6. O. Wedeliana
      dd. Leaf-blades elliptic or oblong-elliptic or oblanceolate.
        e. Leaf-blades membranaceous.
          f. Largest leaf-blades not more than 9.5 cm. broad; lateral nerves 6–9 pairs; petioles to 1 cm. long .... 6. O. Wedeliana
          ff. Largest leaf-blades 10–13 cm. broad; lateral nerves 12–16 pairs; petioles to 1.5 cm. long .... 7. O. atirrensis
        ee. Leaf-blades not membranaceous.
          f. Leaf-blades coriaceous, brownish or castaneous, or greenish, not more than 6.5 cm. broad, reticulation of the upper surface prominulous .... 8. O. Paulii
          ff. Leaf-blades chartaceous, greenish to light brown, up to 10 cm. broad; upper surface very smooth .... 9. O. Dendrodaphne
aa. Largest leaf-blades not more than 17 cm. long.
  b. Leaf-blades variable, usually not obovate, but elliptic, lanceolate-elliptic or oblong, or variations of these shapes, acute or rounded, always chartaceous; margin always finely undulate, appearing crisped on drying; petioles usually blackish; bark grayish; bases not decurrent or recurved .... 10. O. veraguensis
  bb. Leaf-blades not obovate (except sometimes in *O. Austinii*); margin not consistently finely undulate.
    c. Leaf-blades definitely oblong or oblong-elliptic, rigidly coriaceous; inflorescence to 25 cm. long.
      d. Leaf-blades not more than 11 cm. long, densely ferruginous-sericeous beneath; bases decurrent and strongly recurved; inflorescence not more than 8 cm. long .... 11. O. Austinii
      dd. Leaf-blades not less than 12 cm. long, glabrous throughout; bases not decurrent or recurved; inflorescence to 25 cm. long.... 8. O. Paulii
    cc. Leaf-blades not oblong, or if oblong-elliptic, definitely not rigidly coriaceous; inflorescence not more than 15 cm. long.
      d. Leaf-blades coriaceous or subcoriaceous, occasionally chartaceous, the largest usually not less than 6 cm., rarely 5 cm. broad.
        e. Leaf-blades 12–21 cm. long; lateral nerves 6–9 pairs; flowers perfect .... 2. O. Seibertii
        ee. Leaf-blades not more than 16 cm. long; lateral nerves 4–6 pairs; flowers dioecious.

f. Apex of leaf-blades caudate-acuminate; venation rather obscure; reticulation obscure above..........14. O. cernua
ff. Apex of leaf-blades not caudate-acuminate; venation conspicuous and yellowish; reticulation somewhat prominent above..........12. O. rubrinervis
dd. Leaf-blades membranaceous, the largest not more than 4.5 cm. broad..........13. O. subsericea

1. Ocotea Cooperi C. K. Allen in Jour. Arnold Arb. 26:335. 1945.

Tree 18–22.5 m. high; branchlets strongly angled, sulcate, densely ferruginous-tomentose becoming grayish-tomentose. Leaves alternate; petioles stout, pubescent, slightly canaliculate, 1.5 (–2) cm. long; blades glabrous and shining above except for the base of the costa, glaucescent, softly tomentose beneath, brownish olive above, coriaceous, oblong, (15–) 20–35 cm. long and (5–) 9.5 (–11) cm. broad, the base roundish or obtuse, the apex acuminate, penninerved, the costa impressed above, pubescent at the base, beneath robust, strongly elevated and pubescent, the lateral nerves 10–15 pairs, slightly impressed but almost obscure above, fairly well elevated beneath and pubescent, diverging from the costa at an angle of 45–60°, the reticulation prominent throughout. Inflorescence axillary and subterminal, paniculate, to 20 cm. long, ferruginous-tomentose, many-flowered, the apical leaves deciduous, the peduncle to 7 cm. long, ferruginous-tomentose. Flowers to 3 mm. long, the pedicels 2–3 mm. long; perianth-tube urceolate, glutinous within, the lobes yellowish brown or greenish, with unpleasant vegetable-like odor according to the collector, broadly ovate or sub-

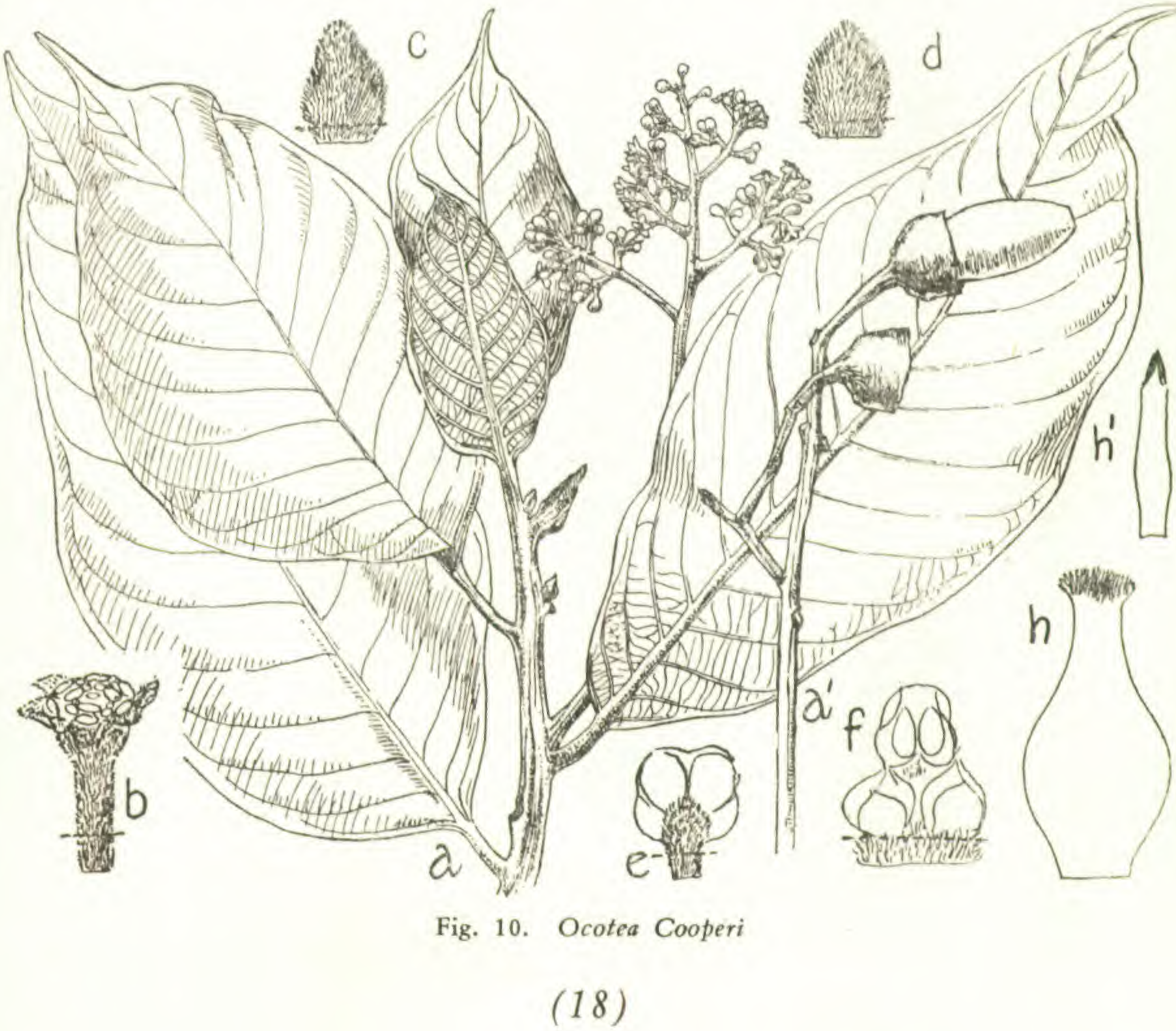

Fig. 10. *Ocotea Cooperi*

triangular, thick or almost ligneous, to 1.7 (–2) mm. long; stamens of ser. I & II broadly spatulate, 0.6 to 1.4 mm. long, the oblong-truncate or square anthers equaling the filaments, the stamens of ser. III to 1.5 mm. long, conspicuously biglandular, the glands sessile and equaling the anthers and filaments; gynaecium glabrous, aborted, or 2.5 mm. or more long, occasionally shorter, the ovary conspicuously stipitate, broadly ovoid, twice the length of the stout style, the stigma triangular, subdiscoid, conspicuous, decurrent on the sides of the style. Fruit ellipsoid, minutely apiculate, 3.5 × 1.8 cm., the subtending cupule ligneous, subhemispherical, rugulose, 1.5 cm. long, 2 cm. in diameter and 11 mm. deep, the margin suberose, thin, supported by a thickened pedicel up to 1 cm. long and 5 mm. in diameter at the apex.

Native to Costa Rica and adjacent Panama at 675–900 meters altitude. Known as "Sweetwood," *Yaya.*

BOCAS DEL TORO: Changuinola Valley, *Cooper & Slater 96 (Y10277);* Cricamola, region of Almirante, *Cooper 498.*

The large, coriaceous, shining leaves and the extremely large and often lignified inflorescence bearing flowers with an urceolate perianth-tube and spatulate anthers at once distinguish this striking species. It is closely associated with *Ocotea stenoneura* from Costa Rica, but the leaf-blades of the latter are conspicuously recurved and decurrent for almost the entire length of the petioles, and the fruits are smaller, globose, and subtended by shallow disk-like undulate-margined cupules.

2. OCOTEA SEIBERTII C. K. Allen in Jour. Arnold Arb. 26:336. 1945.

Tree 22.5–30 m. high; branchlets angled becoming striate or sulcate, gray becoming grayish- and reddish-maculate, early pubescent becoming glabrescent or glabrous. Leaves alternate, glabrous; petioles slender or robust, glabrous, canaliculate, to 12 (–21) mm. long; blades glabrous throughout, except sometimes the costa and nerves near the base beneath, coriaceous, green in the dried state, shining above, only slightly so beneath, elliptic, 12–15 (–21) cm. long and 4.5–6 (–9) cm. broad, the base cuneate, occasionally slightly oblique, the apex slightly obtuse-acuminate, the margin recurved, penninerved, the costa reddish or yellowish, thick and slightly elevated above, prominently so beneath, the nerves 6 (–9) pairs, slightly elevated above, conspicuously so beneath, diverging from the costa at an angle of 45°, the reticulation early conspicuous throughout, presently loose above and prominently and minutely so beneath. Inflorescence axillary, paniculate, to 13 cm. long, pubescent becoming glabrous, reddish, the peduncle to 6 cm. long. Flowers up to 3 mm. long, with slender pedicels of equal length; perianth shallowly infundibuliform, the lobes more or less oblong, subacute or obtuse, thick, pubescent without, densely papillose-pubescent within, 2.8 mm. long; stamens of ser. I & II 1.25 mm. long, the anthers oblong-subrectangular, twice the length of the filaments; those of ser. III to 1.7 mm. long, conspicuously biglandular, the glands one-third the length of the stamens; staminodia subsessile to stipitate, 0.6–0.8 mm. long, ovate, frequently with aborted basal glands; gynaecium

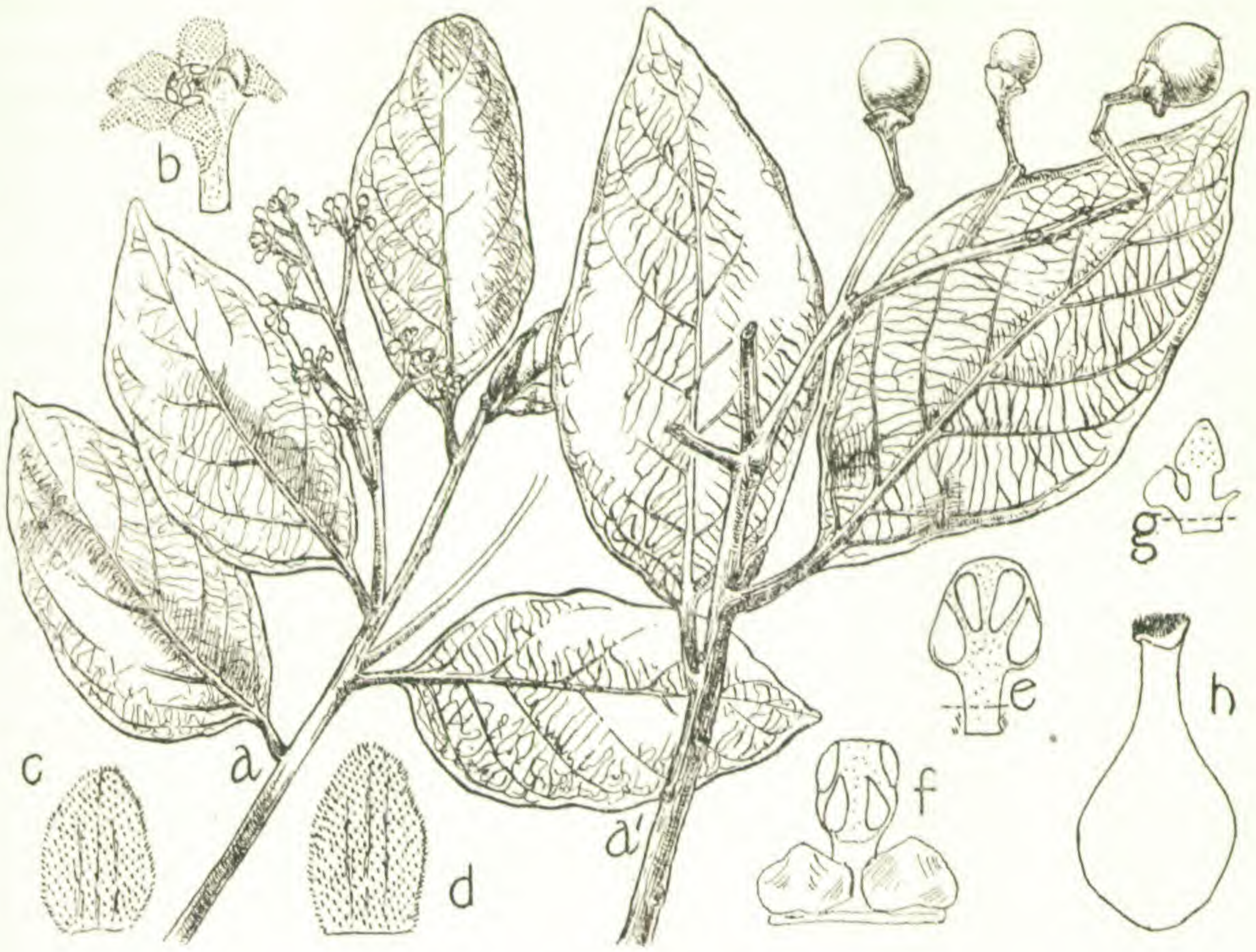

Fig. 11. *Ocotea Seibertii*

glabrous, 2.15 mm. long, the ovary subglobose or obovoid, equaling the style, the stigma conspicuous. Fruit green, globose or slightly obovoid, apiculate, rugulose, 2.3 × 2 cm., the subtending cupule rugulose, glabrous, red, 5 mm. long, 3 mm. in diameter, and 3 mm. deep, the margin undulate, with a well-developed gynophore to 2 mm. long and 6 mm. in diameter, the glabrous pedicel enlarged to 4–8 mm. in length.

Native in the lowland forests of Costa Rica and Panama, up to 2285 meters altitude. Known as *Sigua amarilla*. Good timber tree, with hard wood.

CHIRIQUÍ: Valley of the Upper Río Chiriquí Viejo at Monte Lirio, *Seibert 308;* Chiriquí Viejo Valley, *G. White 96;* Quebrada Velo, vicinity of Finca Lérida, *Allen 4672.*

Near *Ocotea Cooperi,* but lacking the tomentum of the lower leaf-surface. Also, the fruits are obovoid or subglobose.

3. OCOTEA GLOMERATA (Nees) Mez in Jahrb. Bot. Gart. Berlin 5:294. 1889.
Oreodaphne glomerata Nees in Linnaea 21:515. 1848.

Tree or shrub; branchlets thick, conspicuously angled, ferruginous-pubescent, becoming darkened, glabrescent. Leaves alternate, the petioles robust, canaliculate, to 1.5 mm. long; blades glabrous above at maturity, shining, beneath early tomentose becoming glabrescent, glaucescent, coriaceous, usually elliptic to subobovate, 16–25 cm. long and 4–8 cm. broad, the base acute or narrowly attenuate,

with the margin conspicuously recurved, the apex obtusely acute or somewhat acuminate, the margin recurved, penninerved, the costa brownish, slightly elevated above, prominently so beneath, the nerves 12 or more pairs, rather obscure above, slightly elevated beneath, diverging from the costa at an angle of 45°, the reticulation conspicuous throughout, more so beneath. Inflorescences numerous, axillary, paniculate, many-flowered, 15 (–20) cm. long, ferruginous-tomentellous. Staminate flowers 2–3 mm. long, densely pubescent, the pedicels to 1 mm. long; perianth-lobes yellow, broadly ovate, to 3 mm. long; stamens of ser. I & II 1 mm. long, the anthers ovate or ovate-oblong, 2–3 times longer than the filaments; those of ser. III 1 mm. long, oblong-subrectangular, the filaments rather broad, short, with small globose sessile glands; gynaecium glabrous, stipitiform, 1.5 mm. long. Pistillate flowers smaller than the staminate, stamens 1 mm. long, the filaments of the outer series short, the stamens of the inner series almost sessile, the ovary equaling the very thick style, the stigma rather small. Fruit ovoid or ovoid-ellipsoid, apiculate, to 8 mm. long and 4–6 mm. broad, the cupule hemispherical, with entire margin, rugose, to 8 mm. long and 8–9 mm. broad, subtended by a relatively slender pedicel up to 2 mm. long.

Tropical America from Panama and Trinidad, Venezuela, and British Guiana south to Brazil.

CANAL ZONE: without exact locality, *Hayes 1051*.

4. OCOTEA PALMANA Mez & J. D. Smith in Bot. Gaz. 33:258. 1902.

Tree 20 m. high, possibly more; branchlets stout, angled, densely, shortly and minutely ferruginous-tomentose. Leaves alternate; petioles thick, pubescent, striate, to 3 cm. long; blades opaque, glabrous above except for the venation, and beneath densely minutely ferruginous-tomentose, rigidly coriaceous, obovate, to 25 cm. long and 14 cm. broad, the base cuneate, the apex rounded and very shortly abruptly and obtusely acuminate to acutely acuminate, penninerved, the costa broad, scarcely elevated above, prominently so beneath, the nerves 8–10 pairs, slender, delicately and slightly elevated above, conspicuously so beneath, diverging at an angle of 35–55°, the reticulation more or less obscure. Inflorescence stout, axillary, paniculate, about 8 cm. long, densely ferruginous-tomentose, rather few-flowered, the peduncle not more than 2 cm. long. Flowers large, 5–6 mm. long and about 12 mm. in diameter, densely tomentose; perianth-lobes ovate, almost leathery, 2.15–3.8 (–8) mm. long; stamens of ser. I & II 1.25–1.5 mm. long, the anthers ovate or rounded, the filaments short; those of ser. III longer, 1.7–3 mm., the filaments nearly equaling the oblong rounded anthers and completely covered by the large sessile, more or less rounded, basal glands; gynaecium glabrous, usually about 3 mm. long, the ovary ellipsoid or globose, equaling the rather stout, sometimes pubescent style, the stigma capitate or triangular. Fruit green, ellipsoid, oblong, to 3.5 × 1.6 cm., the subtending cupule pink, subcampanulate, to 6 mm. long, 15 mm. in diameter and 5 mm. deep, the margin very thin, the pedicel nearly 2.5 cm. long and expanded to nearly 1 cm. in diameter at the apex.

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Fig. 12. *Ocotea palmana*

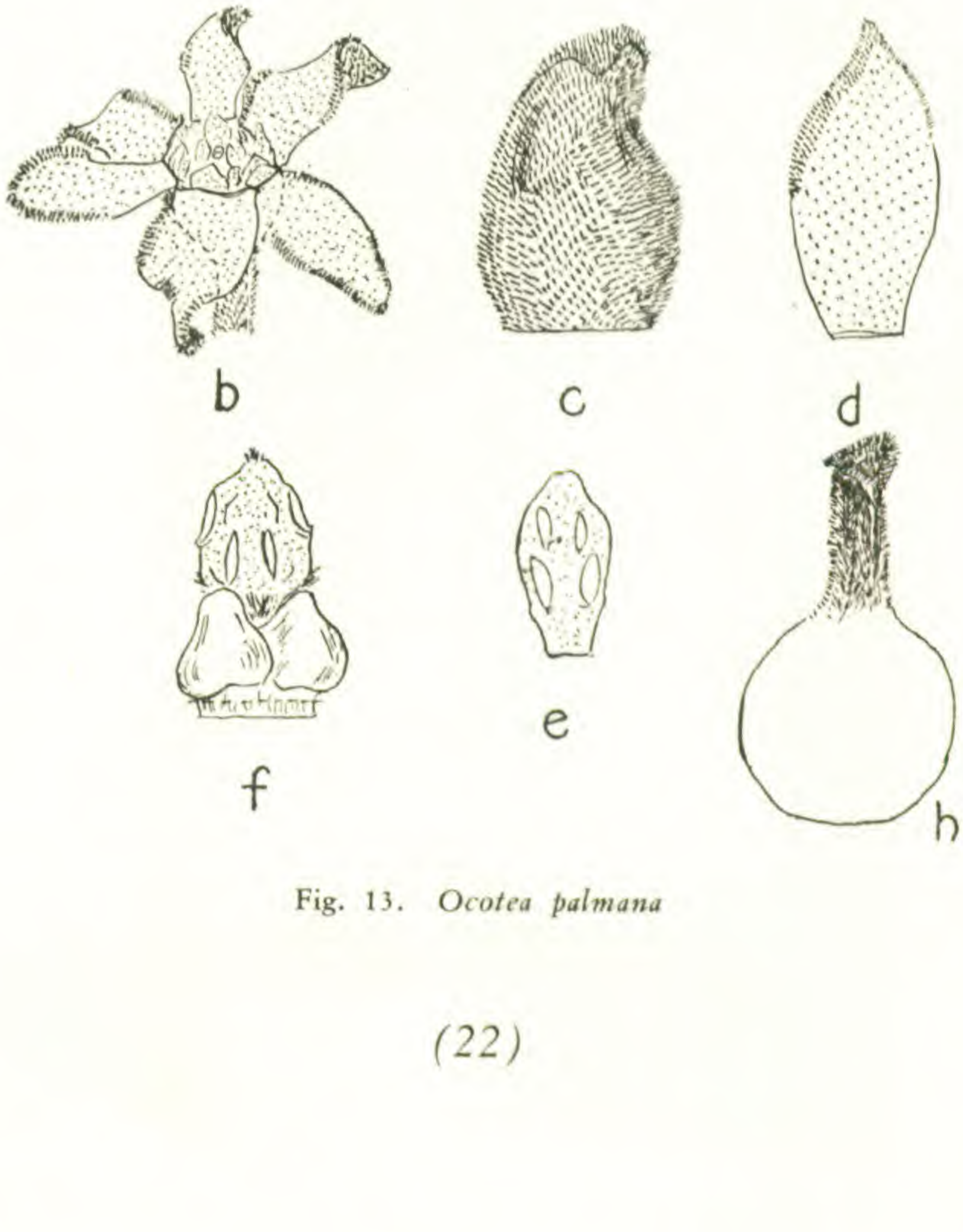

Fig. 13. *Ocotea palmana*

Native of Costa Rica and Panama at about 1500 meters altitude.

BOCAS DEL TORO: Fish Creek Mts., vicinity of Chiriquí Lagoon, *von Wedel 2264.*

This stout robust species stands out because of the large obovate leaf-blades that are rigidly coriaceous, are covered beneath with a dense fine close ferruginous tomentum, and have 8–10 pairs of slender lateral nerves delicately elevated above and conspicuously so beneath. The large densely tomentose flowers with rough almost leathery lobes are also outstanding.

5. OCOTEA IRA Mez & Pittier ex Mez in Bull. Herb. Boiss. II. 3:232. 1903.

Tree? 6–20 m. high; branchlets angled, darkish, early closely appressed, brownish-, almost sericeous-pubescent, becoming glabrous. Leaves alternate; petioles strongly or slightly winged, up to 1 cm. long, or the decurrent recurved blade forming an apparent petiole of nearly 4 cm.; blades glabrous to glabrescent, with frequently inconspicuous axillary glands, opaque, subcoriaceous to rigid, obovate, to 25 cm. long and 9.5 cm. broad, the base cuneate and recurved, the apex abruptly and obtusely acuminate, penninerved, the costa broad and conspicuous although slightly impressed above, prominently elevated beneath, the nerves slender, 9–12 pairs, very slightly elevated above, more so beneath, diverging at an angle of about 35–45°, curving toward the marginal region, the reticulation inconspicuous above and frequently pubescent beneath. Inflorescence axillary and subterminal, panic-

Fig. 14. *Ocotea Ira*

ulate, to 15 cm. long, brownish-pubescent, becoming glabrous, many-flowered, the stout peduncle to 7 cm. long. Flowers small, 2.15 mm. long, equaling the slender pedicel in length, the perianth pubescent without, the lobes thick, papillose, ovate, acute, to 1.4 mm. long; stamens of ser. I & II 0.8–1.25 mm. long, the anthers ovate, obtuse, scarcely longer than the slender filaments; those of ser. III 1–1.7 mm. long, the anthers subrectangular, truncate, not quite equaling the pubescent filaments, glands subglobose, subsessile, sometimes to one-half the length of the filaments; gynaecium glabrous, up to 1.4–2.4 mm. long, the ovary subellipsoid, slightly longer than the slender style, the stigma subtriangular, subdiscoid. Fruit unknown.

Native to Costa Rica and adjacent Panama, in the lowlands, at not more than 200 meters altitude. Known as *Aguacatón.*

BOCAS DEL TORO: region of Almirante, Cricamola Valley, *Cooper 532;* Water Valley, *von Wedel 720;* vicinity of Chiriquí Lagoon, *von Wedel 1382.* CHIRIQUÍ: in lowlands, *Cooper & Slater 218 (Y 10571)*; Progreso, *Cooper & Slater 309 (Y 10660).*

Resembles *Ocotea Tonduzii* and its allies in the shape of the leaf-blades and the decurrent leaf-bases, but the leaf-blades are much larger on the whole than those of O. *Tonduzii.*

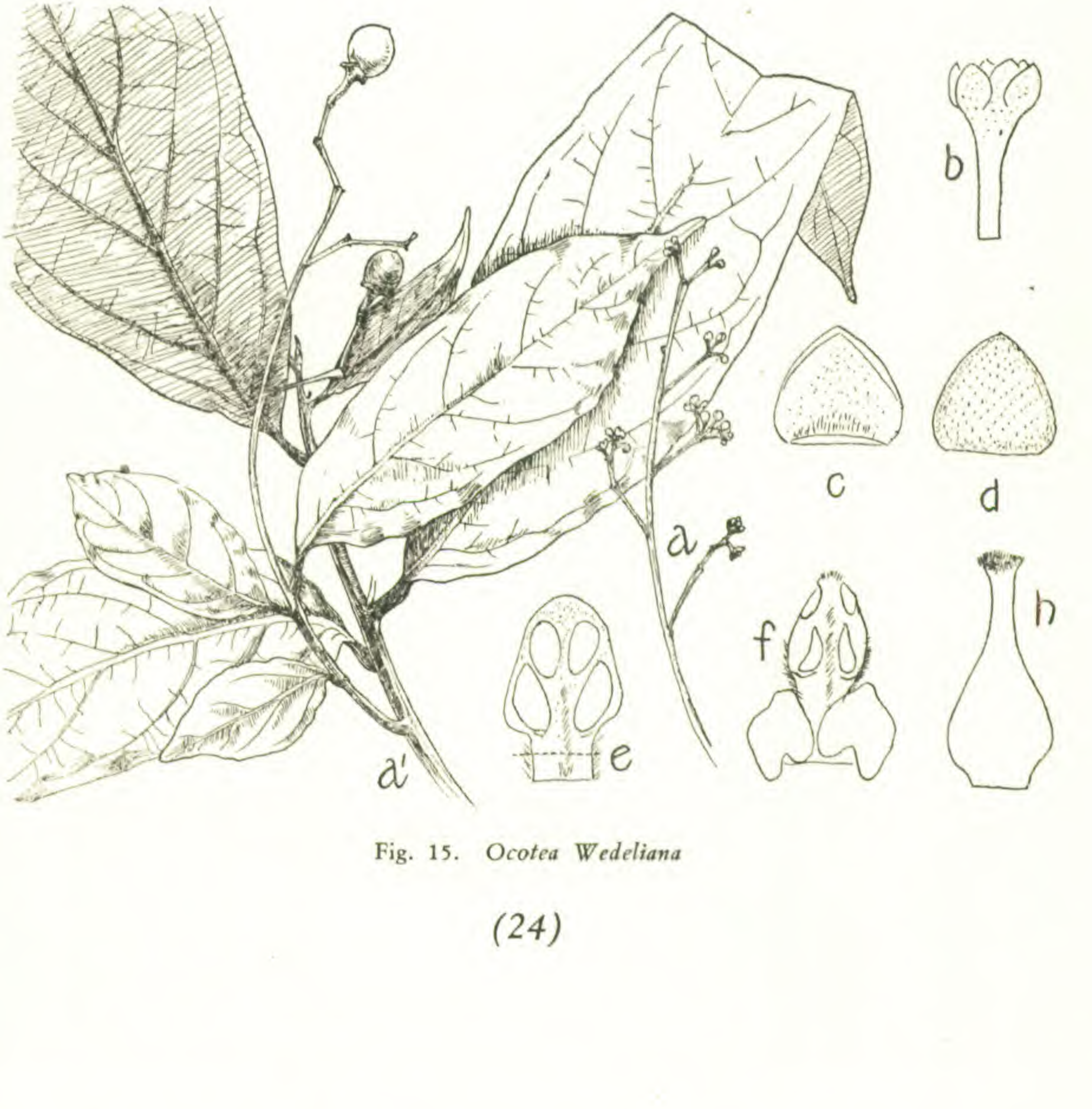

Fig. 15. *Ocotea Wedeliana*

6. OCOTEA WEDELIANA C. K. Allen in Jour. Arnold Arb. 26:339. 1945.

Tree 3–12 m. high; branchlets more or less angled or alate, brown, reddish or gray, minutely and inconspicuously pubescent becoming glabrous. Leaves alternate; petioles often stout, canaliculate, pubescent, to 1 cm. long; blades early fulvous-sericeous, quickly glabrous, membranaceous, opaque, obovate or elliptic, to 26 cm. long and 9.5 cm. broad, base cuneate, apex obtuse, acuminate or long-caudate-acuminate, penninerved, the costa impressed above, elevated beneath, the lateral nerves 6–8 (or 9) pairs, slightly elevated above, prominently so beneath, diverging from the costa at an angle of 35–45°, the reticulation obscure above, rather prominulous beneath. Inflorescence axillary or subterminal, paniculate, to 12 cm. long, glabrescent, few-flowered, the peduncle slender, up to 7.5 cm. long. Flowers to 3.5 mm. long, the slender pedicels to 4.5 mm. long; perianth fulvous-pubescent, the tube conspicuous, the lobes broadly ovate, acute, thick, to 2.15 mm. long; stamens of ser. I & II 1.25–1.7 mm. long, the anthers ovate, obtuse, 3–4 times longer than the stout pubescent filaments; those of ser. III 1.5–2 mm. long, the anthers narrowly ovate, pubescent at the base, twice the length of the filaments, the glands reniform, conspicuous, sessile, equaling the filaments; gynaecium glabrous, 1.7–2.15 mm. long, the subglobose to ovoid ovary equaling the slender style, the stigma conspicuous, discoid. Fruit green, globose, glabrous, to 1 cm. in diameter, the subtending cupule shallow, undulate, red, to 2 mm. long, 8 mm. in diameter and 2 mm. deep, the pedicel red, glabrous, to 8 mm. long and enlarged to 2 mm. in diameter at the apex.

Found to date only from northern Panama, at 375 meters altitude. Known as *Sigua*.

BOCAS DEL TORO: without locality, *von Wedel 388, Cooper 399, 399a;* Buena Vista Camp, on Chiriquí Trail, *Cooper 603 (Y 12236)*. COLÓN: vicinity of Cerro Jefe, *Allen 3439*.

Similar in foliage and floral characters to *Ocotea nicaraguensis* from Nicaragua and Costa Rica, but differs in the texture and size of the leaf-blades. Possibly to *O. nicaraguensis* belongs *Allen* No. *3709*, a fruiting specimen collected north of El Valle de Anton in the province of Coclé, at an altitude of 1000 meters. This number, however, has leaves much smaller than those usually found in *O. nicaraguensis*.

7. OCOTEA ATIRRENSIS Mez & J. D. Smith ex Mez in Bot. Jahrb. 30, Beibl. 67:18. 1901.

Shrub? 3–5 m.; branchlets angled, reddish, early densely minutely ferruginous-pubescent, quickly glabrescent or glabrous. Leaves alternate; petioles stout, canaliculate, glabrescent except for residue of dense pubescence in groove, to 1.5 cm. long; blades glabrous to glabrescent, membranaceous, opaque above, darker beneath, oblong or oblanceolate-elliptic, to 38 cm. long and 6–10 (–13) cm. broad, the base roundish, obtuse or obtusely cuneate, the apex caudate-acuminate, penninerved, the costa broad, impressed above, the lateral nerves 12–16 pairs,

Fig. 16. *Ocotea atirrensis*

rather obscure above, prominently elevated beneath, diverging from the costa at an angle of 45°, the reticulation visible, only slightly elevated above, more prominently so beneath. Inflorescence axillary, paniculate, 15–20 cm. long, pubescent becoming glabrescent, the peduncle to 8 cm. long. Flowers to 3 mm. long, glabrescent, the pedicel glabrescent, not more than 2 mm. long, the perianth-tube well defined, the lobes ovate-elliptic or even broadly ovate, obtuse, somewhat thin, papillose within, 1.25 mm. long; stamens of ser. I & II 0.8 to 1 mm. long, the anthers ovate, subrotund or obtuse, twice the length of the filaments; those of ser. III 1.25–1.7 mm. long, the anthers ovate, obtuse, the slightly shorter filaments bearing sessile subreniform basal glands; gynaecium glabrous, 1.7–2 mm. long, the ovary ovoid to subglobose, equaling the style, the stigma usually inconspicuous, obtuse. Fruit black, fleshy, ellipsoid, 3.3 × 1.5 cm., the subtending cupule shallow, disk-like, the margin undulate, 8 mm. long, 8 mm. in diameter, and less than 2 mm. deep, the pedicel very short, slightly enlarged to 2 mm. at the apex.

Occurs in Costa Rica and adjacent Panama, usually between 600 and 850 meters, occasionally to 1550 meters altitude. Known as *Quizarra* in Costa Rica. Often myrmecophilous.

BOCAS DEL TORO: vicinity of Chiriquí Lagoon, *von Wedel 1399*.

A striking species, because of the very long-acuminate caudate, membranaceous, oblanceolate leaf-blades. More nearly related to *Ocotea Paulii*, but separated readily by the texture and reticulation of the leaf-blades.

Fig. 17. *Ocotea Paulii*

8. Ocotea Paulii C. K. Allen in Jour. Arnold Arb. 26:345. 1945.

Tree (or scandent shrub?) to 15 m. high; branchlets angled, brown becoming gray, sulcate, glabrous. Leaves alternate or subopposite, glabrous; petioles stout, glabrous, reddish black, 1 (–1.5) cm. long; blades glabrous throughout, coriaceous, more or less greenish brown or castaneous in the dried state, oblong, to 20 cm. long and 5–6.5 cm. broad, the base cuneate, often abruptly so, the apex abruptly and obtusely acuminate or rounded or obtuse, sometimes emarginate, penninerved, the costa uniformly thick, reddish, somewhat elevated above, conspicuously so beneath, the nerves 8–12 pairs, inconspicuously elevated above, conspicuously so beneath, diverging from the costa at an angle of 45°, the reticulation somewhat prominulous throughout. Inflorescence axillary or subterminal, broadly paniculate, to 25 cm. long, glabrescent, reddish, many-flowered, peduncle reddish, to 6 cm. long. Flowers to 2 mm. long, pedicels slender, to 2 mm. long, perianth campanulate, pale yellowish, lobes broadly ovate, obtuse, or subacute, membranaceous, 1.25–1.5 mm. long; stamens of ser. I & II 1 mm. long, the anthers ovate, twice the length of the filaments; those of ser. III 1.25–1.7 mm. long, the anthers ovate-quadrate, the glands stipitate; gynaecium glabrous, 1.7 mm. long, ovary broadly ovoid or subglobose, equaling the style, the stigma conspicuous. Fruit black on drying, oblong, 18–20 × 10–11 mm., the subtending cupule shallow, subhypocrateriform, rugulose, glabrous, 2 mm. long, 5–6 mm. in diameter, and 1 mm.

deep, the margin undulate, the pedicel somewhat enlarged, glabrous, 3–4 mm. long.

Costa Rica, in cloud-forests of the Pacific watershed, up to 1450 meters altitude, and Panama up to 1100 meters.

CHIRIQUÍ: between Cerro Vaca and Hato del Loro, *Pittier 5395*. COCLÉ: vicinity of El Valle, *Allen 1211, 1775, 2848*.

Distinguished by the coriaceous leaf-blades, which are bright brown on drying.

9. OCOTEA DENDRODAPHNE Mez in Jahrb. Bot. Gart. Berlin 5:238. 1889.

Dendrodaphne macrophylla Beurling in Vet. Akad. Handl. Stockholm 1854:145. 1856.

Small shrub to tree, to 22.5 m. high; branchlets angled, usually silvery gray, early closely minutely pubescent, quickly becoming glabrous. Leaves alternate; petioles glabrous, stout, canaliculate, blackish, presenting a striking contrast to the pale branchlets, up to 2 cm. long; blades glabrous throughout, or with a few dark hairs persisting at the base on the lower surface, chartaceous, usually pale green to light brown in the dried state, elliptic or oblong-elliptic, to 30 cm. long and 10 cm. broad, the base obtuse or abruptly cuneate, rarely rounded and abruptly cuneate, the apex variable, obtuse or acutish, or even acuminate to caudate-acuminate, penninerved, the costa robust, slightly impressed above and prominently elevated beneath, the lateral nerves to 9 or 10 pairs, delicately and imperceptibly elevated above and more prominently beneath, diverging at an angle

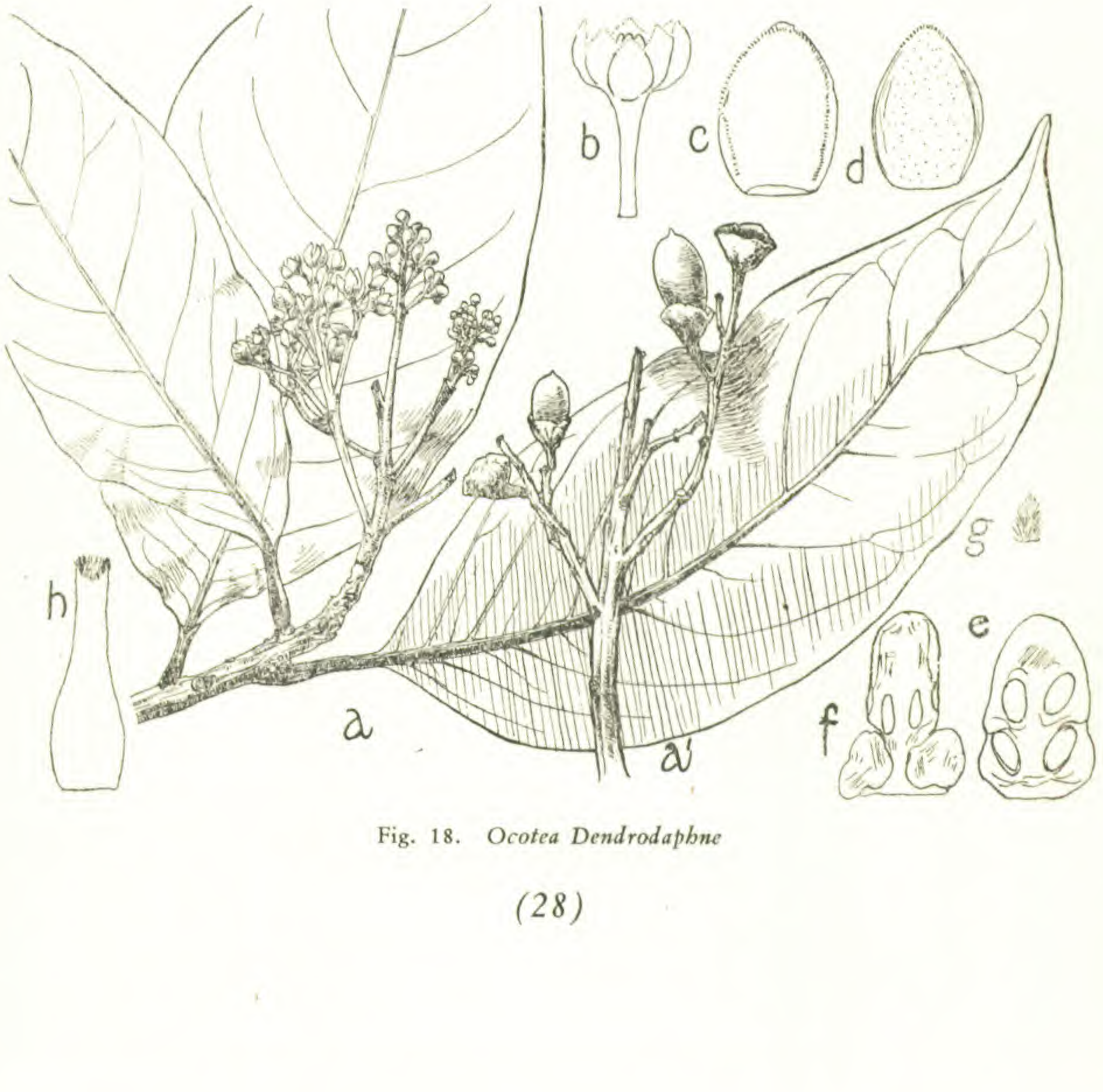

Fig. 18. *Ocotea Dendrodaphne*

of about 45°, the upper surface very smooth, the lower minutely and densely reticulate. Inflorescences numerous, subterminal, panicles 5–10 (–15) cm. long, pubescent, much-branched, many-flowered, the peduncles not more than 4.5 cm. long, usually less. Flowers variable, (3–) 4–6 mm. long, perianth-lobes elliptic, oblong, or ovate-elliptic, fleshy, papillose, 3–5 mm. long; stamens of ser. I & II 1.7–2.8 mm. long, the anthers ovate, acutish or obtuse, petaloid with conspicuous connective tissue one-third their length, the filaments short, stout; those of ser. III 1.7–3.2 mm. long, the filaments longer, the glands small, subsessile; staminodia, if present, variable, subsessile, triangular or cordate, pubescent to glabrous, to 0.6 mm. long; gynaecium glabrous, 2.15–2.4 mm. long, the ovary probably ovoid, the style stout, the stigma usually conspicuous, capitate or decurrent. Fruit black, ellipsoid, 2.3 × 1.2 cm., the subtending cupule cyathiform, woody, glabrous, 1 cm. long, 14 mm. in diameter and 6 mm. deep, the double margin slightly undulate and obscurely lobed, the pedicel rather thick, striate, pubescent to glabrous, to 6 mm. long.

Widespread from Mexico through Guatemala, Honduras, Costa Rica, and Panama from 200 to about 1250 meters altitude.

COCLÉ: hills north of El Valle de Anton, vicinity of La Mesa, *Allen 2299*.

Outstanding because of the silvery gray angled branchlets and stout blackish petioles, which subtend pale greenish leaf-blades that are unusual in that they show no reticulation on their upper surface. The fruits are borne in cupules which show a tendency toward a double margin. The species is similar to *Ocotea veraguensis,* in the cupule character, the blackish petioles, and the gray angled branchlets.

10. OCOTEA VERAGUENSIS (Meissner) Mez in Jahrb. Bot. Gart. Berlin 5:240. 1889.

Sassafridium veraguense Meissn. in DC. Prodr. 15^1:171. 1864.

Tree or shrub 3–10 m. high; branchlets finely gray- or tawny-sericeous, quickly becoming pale gray, glabrous, striate. Leaves alternate or subopposite; petioles stout, canaliculate, blackish, glabrescent, to 1 (–1.5) cm. long; blades early soft grayish-pubescent beneath, becoming entirely glabrous, chartaceous, usually uniformly pale grayish green, the upper surface very smooth, elliptic, lanceolate-elliptic, oblong, oblong-elliptic, rarely obovate, variable in size, (4–) 9 (–13) cm. long and (2–) 4 (–7) cm. broad, the base obtuse or cuneate, the apex rounded-obtuse or obtusely acute, the margin in the dried state usually conspicuously minutely undulate or crisped, penninerved, the costa very prominent above and beneath, although only slightly elevated above and more conspicuously so beneath, the nerves 6 or more pairs, obscure above, only faintly visible beneath, the reticulation also obscure. Inflorescence axillary, paniculate, 3–13 cm. long, grayish-pubescent to glabrescent, many-flowered, the ultimate branchlets frequently giving

the appearance of a capitulum, the peduncle up to 4–6 (–9) cm. long. Flowers to 5 mm. long, more than twice that in diameter at anthesis, pubescent, pedicels slender, pubescent, to 6 mm. or more long; perianth-tube well developed, the lobes oblong or elliptic, obtuse or acutish, thick, fleshy, papillose, to 3–3.5 mm. long; stamens of ser. I & II 2.4 mm. long, anthers petaloid, obovate, nearly sessile, the protruding papillose connective more than one-third the entire length; those of ser. III longer, the anthers with short filaments, the glands conspicuous, short-

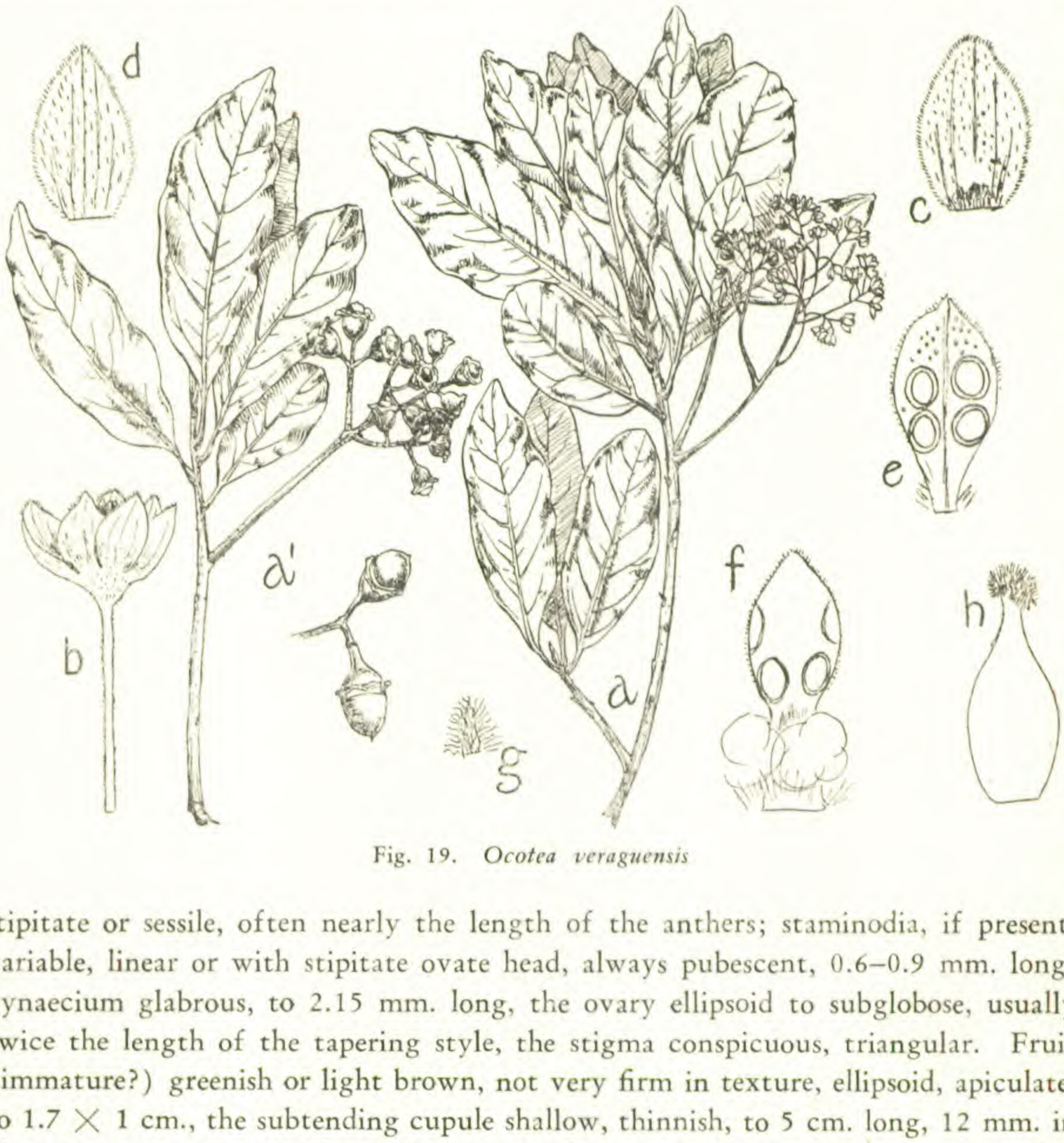

Fig. 19. *Ocotea veraguensis*

stipitate or sessile, often nearly the length of the anthers; staminodia, if present, variable, linear or with stipitate ovate head, always pubescent, 0.6–0.9 mm. long; gynaecium glabrous, to 2.15 mm. long, the ovary ellipsoid to subglobose, usually twice the length of the tapering style, the stigma conspicuous, triangular. Fruit (immature?) greenish or light brown, not very firm in texture, ellipsoid, apiculate, to 1.7 × 1 cm., the subtending cupule shallow, thinnish, to 5 cm. long, 12 mm. in diameter and 3–4 mm. deep, the margin distinctly double, the outer somewhat thickened and undulate, the inner plane, paler in color, minutely pubescent, and protruding beyond the outer for less than 1 mm., the pedicel to 1 cm. long, enlarging towards the apex to about 3 mm. in diameter.

General in forests throughout the coastal regions from Mexico to Panama (Pacific *tierra caliente*), usually at very low altitudes (to 120 meters), occasionally inland as high as 1200 meters. The wood is used in some localities for construc-

tion. Some parts of the tree are used by the natives of Nicaragua as a tonic. Known by a variety of native names in each locality, *Sigua canelo* in Panama.

CHIRIQUÍ: vicinity of San Felix, *Pittier 5278;* along river bank, east of Gualaca, *Allen 5038.* VERAGUAS: "near Veraguas," *Warscewicz 174.* COCLÉ: Penonomé and vicinity, *Williams 236.* PANAMÁ: Río Las Lajas, *Allen 1611.*

For affinities, see the preceding species.

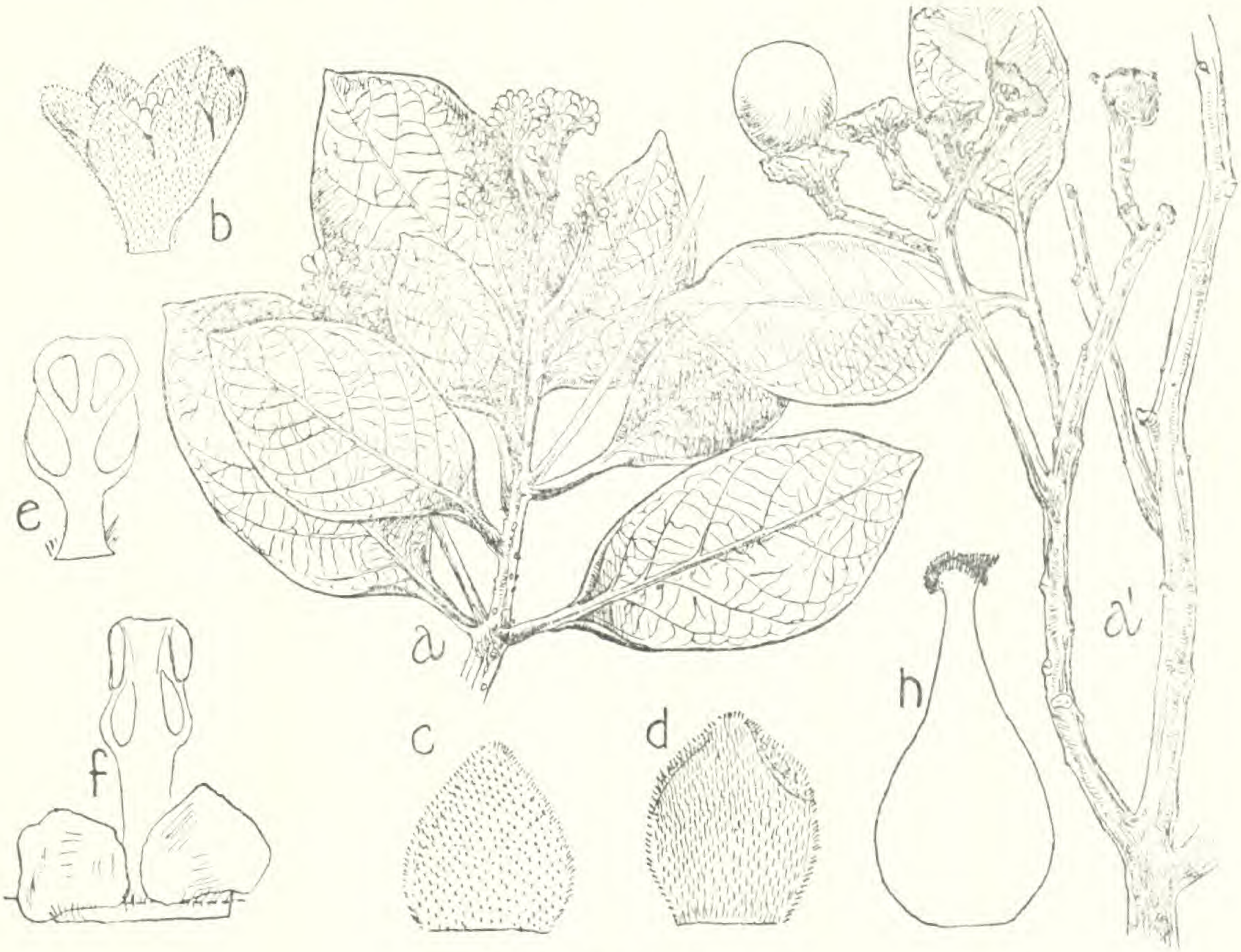

Fig. 20. *Ocotea Austinii*

11. OCOTEA AUSTINII Allen in Jour. Arnold Arb. 26:350. 1945.

Tree 10–18 m. high; branchlets striate, early minutely brown-sericeous-pubescent, becoming gray- or black-pubescent, eventually glabrescent. Leaves alternate, subverticillate; petioles winged, thick, pubescent, 1.5 (–2.5) cm. long; blades early glabrous above, except for the dense and thick ferruginous-sericeous pubescence on the strongly recurved margin and costa beneath, coriaceous, in the dried state brown above or greenish brown, shining, ferruginous-pubescent beneath, opaque, oblong-elliptic, elliptic, or slightly obovate-elliptic, (3–) 7.5–9 (–11) cm. long and (1.8–) 3–4.5 cm. broad, the base cuneate, strongly recurved and decurrent into the petiole, the apex obtuse or slightly and obtusely subacuminate, penninerved, the costa somewhat elevated above, conspicuously so beneath, pubescent throughout, the nerves 7–10 pairs, plane and regularly slightly elevated, concolorous above, obscure, pubescent beneath, diverging at an angle of 45°, frequently obscure glands present in axils of lateral nerves, the reticulation plane

above and regularly subcancellate, elevated. Inflorescence axillary, narrowly paniculate, subcapitate, to 8 cm. long and 2 cm. broad, few-flowered, stout, densely sericeous-ferruginous-pubescent, the peduncle 3–5 cm. long. Flowers 5.5 mm. long, sessile or pedicellate, the pedicels to 2.5 mm. long, the perianth campanulate (urceolate-campanulate, according to the collector), sulphur-yellow, greenish yellow, or occasionally white, the lobes broadly ovate, acute, thick, densely pubescent, 3–3.5 mm. long; stamens of ser. I & II to 1.9 mm. long, the anthers equaling or twice the length of the filaments; those of ser. III 2.15–2.5 mm. long, the glands sessile, nearly equaling the anthers; gynaecium glabrous, 2.5–3 mm. long, the ovary subglobose or ovoid, more than one-half the entire length, the stigma triangular, conspicuous. Fruit black-olivaceous, minutely canescent or gray-canescent-punctate according to the collector, broadly obovoid, 28–30 × 20–22 mm., the subtending cupule shallow, red, subcampanulate or at maturity sometimes infundibuliform, somewhat verruculose, glabrous or glabrescent, rugulose, 6–7 cm. long, to 1.5 cm. in diameter and 3 mm. deep, the pedicel glabrous, rugulose, aciculate, to 1 cm. long.

Occurs in cloud-forests or cleared pasture-land of Costa Rica and in rain- and cloud-forests of the adjacent areas of Panama, at an altitude of 1765 to 2300 meters in Costa Rica and up to 1980 meters in Panama. Wood used for lumber. Known as *Sigua Canela*.

CHIRIQUÍ: in rain-forest, Bajo Chorro, Boquete, *Davidson 268;* cloud-forest, Cerro Horqueta, *von Hagen & von Hagen 2128;* Bajo Mona, Robalo Trail, western slope of Cerro Horqueta, *Allen 4846;* vicinity of Cerro Punta, *Allen 3508* (a robust form, seemingly).

Distinct because of the very prominent and regular, more or less cancellate reticulation of the leaf-blades, the lower surface of which is glaucescent, with sericeous pubescence. These characteristics separate the species from *Ocotea Tonduzii, O. Endresiana,* and *O. Skutchii,* its nearest relatives.

12. Ocotea rubrinervis Mez in Jahrb. Bot. Gart. Berlin 5:351. 1889.

Tree or shrub 4.5–12 m. high; branchlets dark brown, pubescent becoming glabrous, cinereous, terete. Leaves alternate; petioles pubescent becoming glabrescent, canaliculate, to 1 cm. long; blades scattered, pubescent near the base above, glabrescent beneath except for pubescent axillary glands, subcoriaceous, elliptic or broadly elliptic, to 11 cm. long and up to 7 cm. broad, the base roundish, obtuse or cuneate, the apex shortly obtusely acuminate or obtusely acute, penninerved, the costa impressed above and prominently elevated and yellowish beneath, the lateral nerves 4–6 pairs, also impressed above and prominently elevated and yellowish beneath, diverging at an angle of about 55°, somewhat reticulate above. Inflorescence axillary or subterminal, paniculate, with narrowly racemose branchlets, to 6–9 (–15) cm. long, glabrescent for the most part, the peduncle very short, occasionally to 3 cm. long. Staminate flowers to 3 mm. long, sessile or with short pedicels to 1 mm. long; perianth yellow, grayish- or ferruginous-pubescent, the lobes ovate, acutish, rather thick, about 2.15–2.5 mm. long; the stamens of ser.

Fig. 21. *Ocotea rubrinervis*

I & II to 1.5 mm. long, the anthers ovate, obtuse to roundish, longer than the filaments; those of ser. III slightly larger, the anthers more narrowly ovate, the filaments completely covered on the dorsal side by the fused sessile glands borne at their bases; staminodia slender, transparent, less than 0.5 mm. long, oblanceolate; gynaecium glabrous, aborted, to 1.9 mm. long, subcylindrical, the stigma subpeltate, depressed above. Pistillate flowers unknown. Fruit green, in the dried state blackish or greenish, ellipsoid, apiculate, rugulose, 11 $\times$ 8 mm., the subtending cupule campanulate, 6-lobed, with the lobes more or less horizontally spreading, somewhat papyraceous, not more than 1.5 mm. long, the entire cupule pubescent or glabrescent, green or red according to the collector, 6–7 mm. long, 8 mm. in diameter, and 2–3 mm. deep, usually sessile.

Described originally from Panama, the locality unknown, and from San Martín, Peru. Now known to occur as far south as Bolivia, at altitudes of less than 1000 meters.

PANAMÁ: San José Island, Perlas Archipelago, Gulf of Panama, *Johnston 111, 133, 250, 415, 497, 556, 563, 604, 655.*

Outstanding among Panamanian species because of the very prominently elevated venation beneath, and the almost spike-like few-flowered panicles.

13. Ocotea subsericea Standley in Field Mus. Publ. Bot. 18:456. 1937.

Shrubby tree to 6 m. high; branchlets minutely but densely appressed, yellowish-buff-sericeous-tomentose, angled, becoming grayish, glabrous, terete and striate-sulcate. Leaves alternate; petioles slender, subcanaliculate, pubescent, up to 1.5 cm. long; blades early subferruginous-sericeous, quickly glabrescent, thinly membranaceous becoming more thickly membranaceous, elliptic, to 12 cm. long and 4.5 cm. broad, the base cuneate, the apex abruptly and obtusely acuminate, penninerved, the costa minutely elevated above and conspicuously so beneath, the lateral nerves 6–8 pairs, diverging at an angle of about 45°, and bearing more or less conspicuous axillary glands. Inflorescence axillary, paniculate, to 6.5 cm. long, rather few-flowered, densely but closely pubescent. Flowers (possibly staminate?) to 3 mm. long, the pedicels 2–4 mm. long, the perianth spreading, campanulate, glabrescent, the lobes ovate or oblong, acutish, fleshy and papillose within, about 2.15 mm. long; stamens of ser. I & II 1.25 mm. long, the anthers ovate, truncate, almost equaling the stout filaments; the anthers of ser. III oblong, the filaments covered almost completely by the two conspicuous sessile basal glands; staminodia, if present, very small; gynaecium (either undeveloped or the aborted gynaecium of a staminate flower of a dioecious tree) glabrous, slender, about 2.15 mm. long, the ovary narrow, blending almost imperceptibly into the stout style, the stigma conspicuous, peltate or subtriangular. Fruit black, pointedly ovoid, to 2.5 × 1.5 cm.

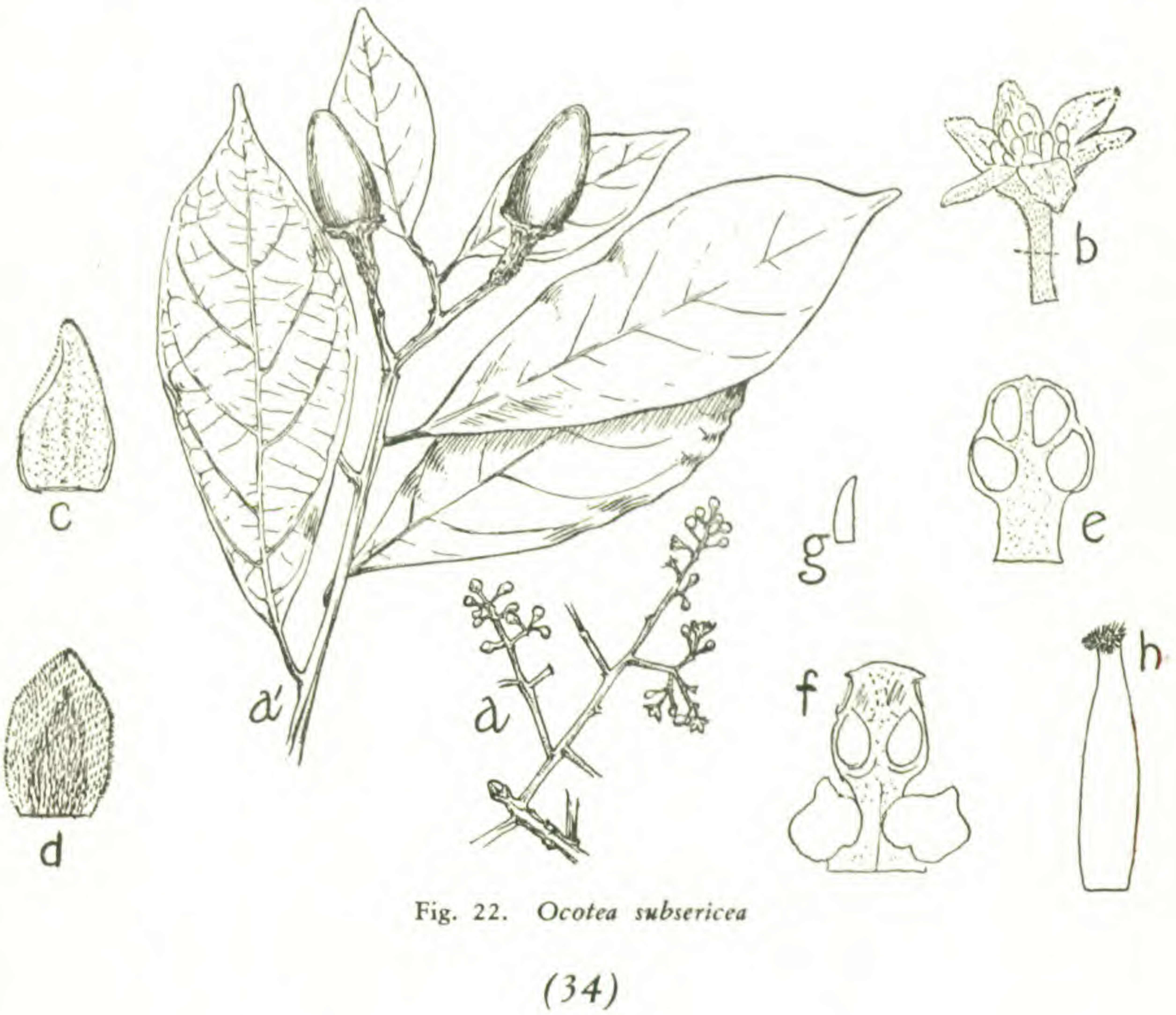

Fig. 22. *Ocotea subsericea*

near the base, the subtending cupule flat, almost disk-like, woody, pale brownish buff, separating, on drying at least, from the fleshy fruit, about 1.5 cm. in diameter and slightly undulate, the enlarged pedicel pale brownish buff, deeply furrowed and verruculose, to 1 cm. long, and 5 mm. in diameter throughout.

Costa Rica and Panama, at an altitude of about 1250 meters.

COCLÉ: north rim of El Valle, *Allen 1907*.

The pointed fruits with the flat almost disk-like woody cupule set apart this species from others of Panama. The nearest relative is *Ocotea eucuneata* from British Honduras and Guatemala, from which it is distinguished by the smaller leaves and smaller thinner cupule. *Allen* No. *3727*, collected in bud, north of El Valle de Anton, in the province of Coclé, at an altitude of about 1000 meters, possibly belongs to this species. However, the tree is larger, the branchlets less striate, and the leaves more coriaceous.

14. OCOTEA CERNUA (Nees) Mez in Jahrb. Bot. Gart. Berlin 5:377. 1889.

Tree or shrub 3.6–6 m. high; branchlets angled or striate, terete, early pubescent, quickly glabrous. Leaves alternate or subopposite; petioles slender, canaliculate, glabrous, up to 12 mm. long; blades glabrous throughout, chartaceous, or subcoriaceous, oblong-elliptic, to 16 cm. long and 6.5 cm. broad, the base, generally speaking, roundish or obtuse, with the extreme portion abruptly cuneate, the apex

Fig. 23. *Ocotea cernua*

abruptly or gradually acuminate, usually caudate-acuminate, penninerved, the costa conspicuous above, more prominently elevated beneath, the lateral nerves 4–6 pairs, delicate, obscure above, more prominent beneath, the lowermost pairs usually the longest, and diverging at an angle of about 45°, the reticulation obscure above, less so beneath. Inflorescences numerous, axillary, slender, panicles 4–5 (–7.5) cm. long, branching racemosely, many-flowered, glabrous, the peduncle rarely more than 2 cm. long. Staminate flowers small, not more than 2 mm. long, the pedicels slender, filamentous, to 4 mm. long, the perianth-lobes ovate, obtusish or acute, glabrous, (1–) 1.25 (–1.7) mm. long; stamens of ser. I & II 0.8 mm. long, the anthers quadrate or ovate-triangular, obtuse, almost sessile; those of ser. III longer, the anthers more narrowly ovate, the filaments with two basal, compressed, often suborbicular, subsessile glands; gynaecium glabrous, aborted, linear, not more than 0.8 mm. long. Pistillate flowers similar to the staminate; stamens smaller, seemingly sterile; gynaecium glabrous, 1.5 mm. long, the ovary ellipsoid-subglobose, attenuate into an extremely short style, the stigma conspicuous, three-parted. Fruit black, ellipsoid, apiculate, to 14 × 9 mm., the lower third encased in a more or less snug-fitting hemispherical, somewhat woody cupule 6 mm. long, 11 mm. in diameter, and 3–4 mm. deep, the pedicel to 7 mm. long, expanded to 2 mm. in diameter at the apex.

Southern Mexico, Central America, and the West Indies, and, according to Meissner, in South America. Known as *Sigua, Sigua amarillo.*

BOCAS DEL TORO: Changuinola Valley, *Cooper & Slater 105 (Y 10286)*; Island Potrero, *Dunlap 568;* Water Valley, *von Wedel 803.* CHIRIQUÍ: without locality, *Cooper & Slater 262 (Y 10615).* CANAL ZONE: *Hayes 397;* Barro Colorado Island, Shannon Trail, *Shattuck 535;* Drayton Point, *Shattuck 1140;* shore of cove s. from lock site, *Woodworth & Vestal 471.* DARIÉN: along the Sambú River, above tide-limit, *Pittier 5692.*

The only species of the genus in Panama with dioecious flowers. Most nearly related to *Ocotea Bernoulliana,* with perfect flowers, from Guatemala, Honduras, and British Honduras, and to *O. tenera* from Costa Rica, also dioecious, but with fruits larger and subtended by a flat shallow cupule with an undulate margin.

4. NECTANDRA Rollander

NECTANDRA Rollander ex Rottboell in Acta Univ. Hafn. 1:267. 1778.

Evergreen trees or shrubs. Leaves alternate, or occasionally subopposite, the blades penninerved. Inflorescence axillary and/or subterminal, usually paniculate. Flowers perfect, pedicellate. Perianth-tube conspicuous or lacking. Perianth-lobes usually fleshy and reflexed or spreading at anthesis, usually deciduous. Stamens of the two outer series fleshy, petaloid, papillose and ovate, or quadrate or orbicular with conspicuous connective tissue, or reniform or subreniform, frequently emarginate, with no apparent connective tissue, the cells occupying the entire anther. Anthers sessile or borne on filaments, with four introrse cells usually arranged in an arc-like formation, which only rarely is obscure. Stamens of inner

or third series usually quadrate; in flowers bearing petaloid outer series, the inner also sometimes fleshy and papillose with truncate connectives; in other cases, the inner not fleshy nor papillose and the connectives inconspicuous. Four cells arranged in two horizontal planes; those of the upper plane lateral or laterally extrorse; those of the lower plane usually extrorse. Staminodia when present, for the most part, stipe-like. Gynaecium completely glabrous except in *N. reticulata;* ovary subglobose or ovoid, rarely ellipsoid; style usually short; stigma conspicuous, discoid or subcapitate, triangular or occasionally triangular-peltate, often decurrent. Fruit usually ellipsoid or subglobose, occasionally oblong or obovoid, borne in a cupule with simple margin occasionally bearing remnants of the perianth-lobes, uniformly subtended by enlarged pedicel.

Nectandra consists roughly of 175 recognized species, 125 of which are to be found in South America, about 34 in Mexico and Central America, and the remainder in the West Indies. Good timber for carpentry and general construction locally.

a. Leaf-blades not recurved at all at the base or decurrent, not auriculate nor cordate nor even rounded at the base generally.
  b. Largest leaf-blades never more than 8 cm. long.
    c. Largest leaf-blades up to 7 cm. long and 2.2 cm. broad, lanceolate or elliptic-lanceolate, varnished-shining above, the reticulation somewhat obscure.......... 1. N. DAVIDSONIANA
    cc. Largest leaf-blades up to 8 cm. long and 3–4 cm. broad, elliptic, not varnished-shining above, the reticulation very conspicuous.......... 2. N. SMITHII
  bb. Largest leaf-blades never less than 9–10 cm. long.
    c. Anthers of the two outer series of stamens fleshy, petaloid, papillose, never emarginate, the upper third consisting of connective tissue, the remaining space occupied by the cells.
      d. Leaf-blades pale green, usually with the venation and reticulation showing yellowish, often with large ellipsoid axillary pubescent glands on the lower surface, but conspicuous on both surfaces.......... 3. N. PANAMENSIS
      dd. Leaf-blades not pale green with conspicuous whitish venation and reticulation; axillary glands, if present, rather inconspicuous.
        e. Branchlets, leaf-blades, petioles and inflorescences ferruginous-tomentose or ferruginous-tomentellous.
          f. Leaves alternate, the blades elliptic or ovate, the base obtuse, coriaceous, densely tomentose beneath.......... 4. N. LAUREL
          ff. Leaves opposite usually, the blades lanceolate or elliptic, the base acute, rigidly coriaceous, tomentellous beneath.......... 5. N. RIGIDA
        ee. Branchlets, leaf-blades, petioles and inflorescences not ferruginous-tomentose or ferruginous-tomentellous.
          f. Leaf-blades with lateral nerves 8–12 pairs.......... 6. N. GLOBOSA
          ff. Leaf-blades with lateral nerves 4–5 (–7) pairs.......... 7. N. RAMONENSIS
    cc. Anthers of the two outer series of stamens not fleshy, petaloid, or papillose, but quadrate or reniform, subreniform or suborbicular, and frequently emarginate, the cells occupying the entire anther.
      d. Greatest width of leaf-blades at or below the middle, the blade tapering towards the apex only.......... 8. N. GENTLEI
      dd. Greatest width of leaf-blades exactly at the middle or the blade tapering towards the base and the apex equally, or the leaf-blades obovate.
        e. Largest leaf-blades not less than 7 cm. broad.......... 9. N. WOODSONIANA
        ee. Largest leaf-blades not more than 6.5 cm. broad, usually less than 5 cm.

f. Inflorescence usually glabrous; branchlets glabrous or minutely and sparsely pubescent becoming glabrous.
g. Leaf-blades not caudate-acuminate at the apex.............. 10. N. SALICINA
gg. Leaf-blades caudate-acuminate at the apex..................... 11. N. FUSCOBARBATA
ff. Inflorescence variously pubescent; branchlets early densely and minutely golden- or subferruginous-tomentose or sericeous, later becoming glabrescent to glabrous.
g. Reticulation loose, scarcely apparent on the upper surface of the leaf-blades... 12. N. NITIDA
gg. Reticulation minute, exceedingly prominent throughout.. 13. N. LATIFOLIA
aa. Leaf-blades recurved at the base and decurrent, or auriculate and recurved, or cordate and recurved.
b. Base of leaf-blades decurrent and recurved, not auriculate.
c. Petioles not thickened or lengthened by decurrent leaf-blades; leaf-blades only slightly decurrent at the base and very slightly recurved for less than 5 mm.
d. Anthers more or less ovate, obtuse, with fleshy, papillose connectives; fruit ellipsoid or globose.
e. Leaf-blades with lateral nerves 8–12 pairs................................ 6. N. GLOBOSA
ee. Leaf-blades with lateral nerves 4–6 (–7) pairs........................ 7. N. RAMONENSIS
dd. Anthers subreniform, subemarginate; fruit usually globose.
e. Leaf-blades chartaceous, lanceolate, the greatest width at or below the middle, the blade tapering towards the apex only.... 8. N. GENTLEI
ee. Leaf-blades coriaceous, elliptic, the greatest width exactly at the middle, the blade tapering towards the base and the apex equally, or rarely obovate.. 14. N. STANDLEYI
cc. Petioles variously thickened and seemingly lengthened by decurrent leaf-blades; leaf-blades conspicuously decurrent and recurved at the base up to 4–5 cm.
d. Largest leaf-blades not more than 3.5 (–4) cm. broad............. 15. N. WHITEI
dd. Largest leaf-blades not less than 5 cm. broad, usually more than 6 cm.
e. Leaf-blades usually shining above, and heavily reticulate; anthers ovate, the connective tissue comprising the upper ¼–½; stigma borne on a well-defined style; cupule and pedicel to 2.5 cm. long.. 16. N. HYPOGLAUCA
ee. Leaf-blades not shining, inconspicuously reticulate above; anthers subreniform (or depressed-globose), the cells occupying the entire anther; stigma subsessile; cupule and pedicel 1.8 cm. long.. 17. N. PAULII
bb. Base of leaf-blades definitely auriculate and recurved, the recurved auricles often overlapping conspicuously beneath................................ 18. N. RETICULATA

1. NECTANDRA DAVIDSONIANA C. K. Allen in Jour. Arnold Arb. 26:369. 1945.

Tall tree; branchlets foliose, fulvous-sericeous, quickly glabrescent, the bark actually reddish brown, but obscured by a thin grayish epidermis that is deciduous. Leaves alternate; petioles slender, canaliculate, to 8 mm. long; blades glabrous throughout, membranaceous, varnished-shining above in dried state, greenish or brown, paler beneath, lanceolate or elliptic-lanceolate, 5–6 (–7) cm. long and 13–17 (–22) mm. broad, the base cuneate, the apex obtuse or obtusely acuminate, penninerved, the costa inconspicuous above, slightly elevated beneath, the lateral nerves usually 4 pairs, obscure above, slightly elevated beneath, diverging from the costa at an angle of 35–45°, the reticulation inconspicuous above, scarcely conspicuous beneath. Inflorescence axillary, paniculate, small, 2 (–4) cm. long, slender, inconspicuous, glabrous, very few-flowered (to 5), the peduncle slender, glabrous, to 2 (–2.5) mm. long. Flowers to 4 mm. long, the pedicels slender, often up to 3 mm. long, the perianth campanulate, cream-colored, the subequal

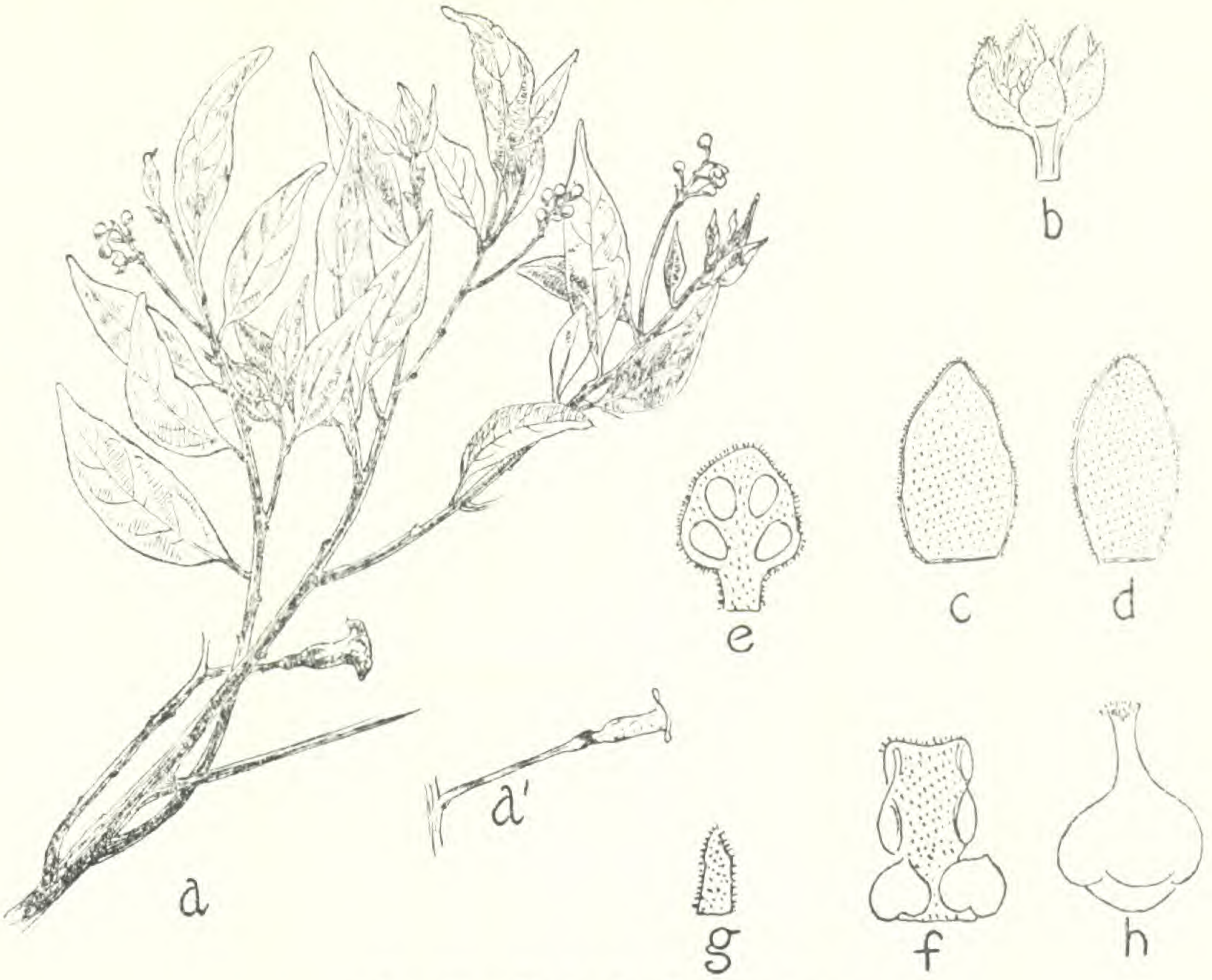

Fig. 24. *Nectandra Davidsoniana*

lobes membranaceous, papillose, elliptic, 2.8 mm. long; stamens of ser. I & II to 1 mm. long, the anthers oblong-globose, three times the length of the slender filaments; those of ser. III 1.25 mm. long, the anthers oblong, the glands short-stiped, sometimes equaling the anthers and filaments; staminodia strap-shaped or triangular, inconspicuous, 6 mm. long; the gynaecium glabrous, 1.5 mm. long, the ovary ovoid or subglobose, three times longer than the stipe and twice the length of the style, the stigma triangular-discoid, conspicuous. Fruit unknown, black according to the collector, the cupule hypocrateriform, disk-like, red according to the collector, glabrous, 1 cm. in diameter, the pedicel subverruculose, to 1 cm. long and 4 mm. in diameter throughout, the margin entire, slightly undulate.

Known only from the type locality in Chiriquí, at 1830 meters altitude.

CHIRIQUÍ: Boquete, *Davidson 564*.

In general aspect resembling *Nectandra salicifolia* from Mexico and northern Central America, but differing in the shape of the anthers, and in the smaller leaves.

2. NECTANDRA SMITHII C. K. Allen in Jour. Arnold Arb. 26:370. 1945.

Tree 10–17 m. high; branchlets foliose, minutely subferruginous-pubescent, gray, striate, verruculose. Leaves alternate; petioles slender, glabrescent, canaliculate, (5–) 7–10 (–12) mm. long; blades glabrous throughout, except the venation at the base of the costa, membranaceous, brown throughout in the dried state,

somewhat shining above, elliptic, 6–8 cm. long and 3–4 cm. broad, the base cuneate, rarely obtuse, the apex acute or shortly subcaudate-acuminate, penninerved, the costa pubescent throughout, conspicuously elevated beneath, the nerves 5 pairs, slightly prominent above, strongly so beneath, diverging at an angle of 35–45°, the axillary glands conspicuous, usually fulvous-pubescent, the reticulation very conspicuous throughout. Inflorescence axillary, paniculate, short, 2–3 (–5.5) cm. long, glabrescent, few-flowered, the peduncle slender, 1–2 cm. long. Flowers to 3.5 mm. long, the pedicels slender, 1.5–2 (–8) mm. long, the perianth subcampanulate, white (?) or cream, the lobes oblong, obtuse, fleshy, papillose-

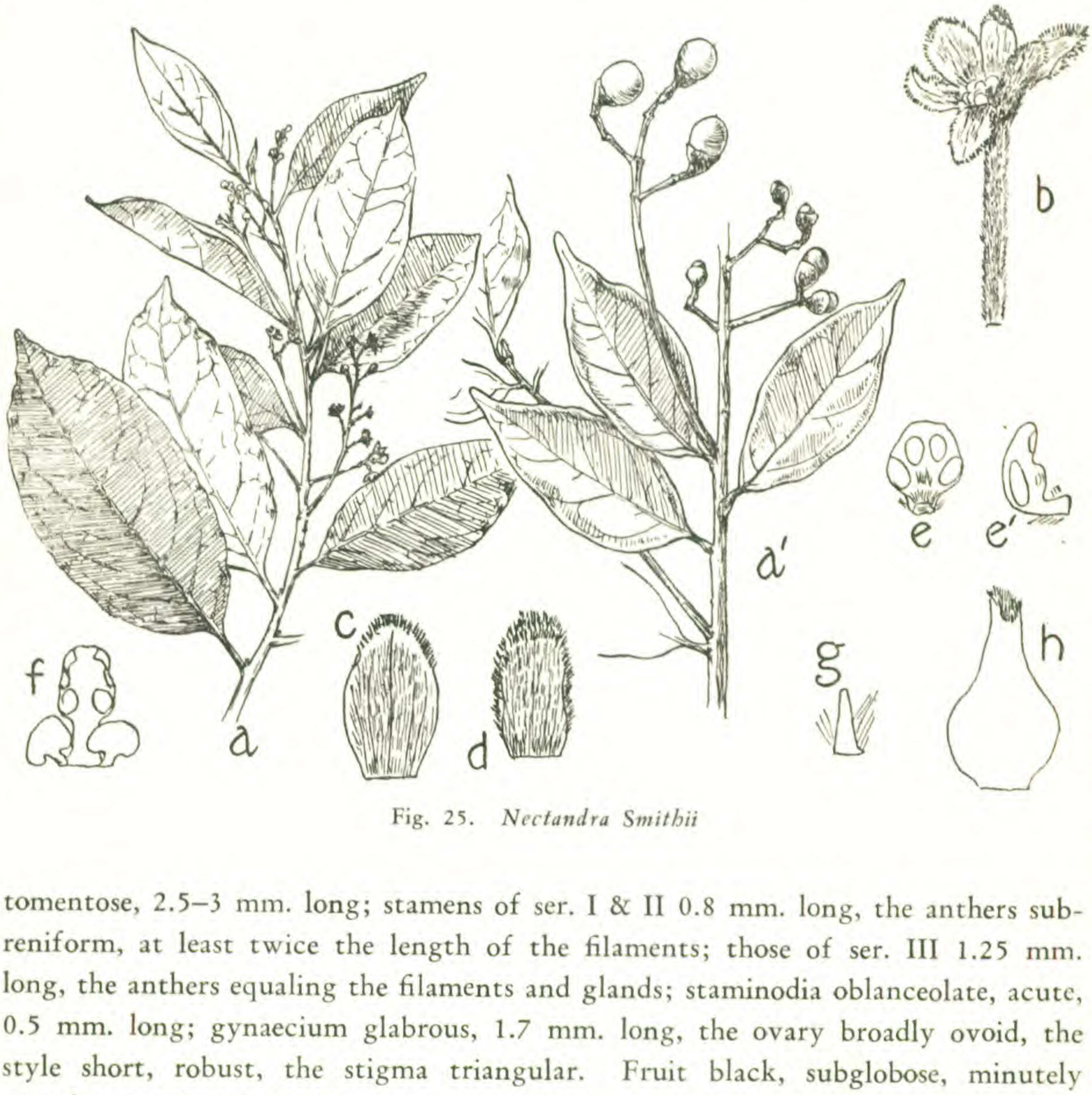

Fig. 25. *Nectandra Smithii*

tomentose, 2.5–3 mm. long; stamens of ser. I & II 0.8 mm. long, the anthers subreniform, at least twice the length of the filaments; those of ser. III 1.25 mm. long, the anthers equaling the filaments and glands; staminodia oblanceolate, acute, 0.5 mm. long; gynaecium glabrous, 1.7 mm. long, the ovary broadly ovoid, the style short, robust, the stigma triangular. Fruit black, subglobose, minutely apiculate, to 1 cm. in diameter, the subtending cupule shallow, tumescent, to 4 mm. long, 6 mm. in diameter and 2 mm. deep, the pedicel 4–5 mm. long, expanded to 3 mm. in diameter at the apex.

Costa Rica, in the Caribbean cloud-forest at 1600–1700 meters altitude and in Panama from 100 to 800 meters.

COCLÉ: vicinity of El Valle, *Allen 774, 3534.* PANAMÁ: residual forest in rolling grassland, trail from Campana to Chica, Cerro Campana, *Allen 2652.*

Also reminiscent of *Nectandra salicifolia*, but distinguished by the very foliose branchlets, the consistently few pairs of lateral nerves, the prominent reticulation of the small leaves, and the bulging cupule which fits snugly about the very base of the fruit.

3. NECTANDRA PANAMENSIS Mez in Jahrb. Bot. Gart. Berlin 5:443. 1889.

Tree to 20 m. or more (or shrub); branchlets glabrous with only a trace of

Fig. 26. *Nectandra panamensis*

pubescence at the apex, greenish becoming brownish, angled becoming terete and striate. Leaves alternate; petioles glabrous, up to 1 cm. long; blades glabrous, membranaceous or chartaceous, pale greenish in the dried state, narrowly elliptic or elliptic-lanceolate, 15 (–20) cm. long and 3.5 (–5.5) cm. broad, the base cuneate, the apex acutish or subacuminate or often obtusely long-acuminate, penninerved, the costa plane and conspicuous above because of its yellowish color, elevated beneath, the nerves 5–7 (–9) pairs, yellowish and slightly elevated above, but more conspicuously so beneath, diverging from the costa at an angle of 25–35 (–45)°, usually with very prominent large ellipsoid pubescent glands beneath, the imprint of which is conspicuous on the upper surface of the blade. Inflorescence axillary or subterminal, paniculate, 12 (–19) cm. long, much-branched near

the base, peduncle very short. Flowers 3.5–4 mm. long and up to 8 mm. in diameter, the pedicel slender, to 4 (–16) mm. long, the perianth white, pubescent, the lobes fleshy, pubescent, up to 3 mm. long; stamens of ser. I & II 0.8 mm. long, the anthers broadly ovate, obtuse or somewhat depressed-globose, the fleshy, papillose connective tissue apparent, the filaments very short and thick; those of ser. III to 1.25 mm. long, the anthers subrectangular, broader than long, the filaments rather stout, the glands conspicuous, sessile, almost larger than the anthers; staminodia very thin, almost scale-like, or ovate, pubescent, to 6 mm. long, the stipe about half the entire length; gynaecium glabrous, 1.7 mm. long, the ovary ellipsoid or subglobose, the style very short, stout, the stigma triangular, conspicuous. Fruit (immature?), with the subtending cupule cyathiform, to 6 mm. long, 9 mm. in diameter, and 4 mm. deep, the pedicel up to 5 mm. long, and scarcely broader at the apex than at the base.

Panama, from 30 to 100 meters altitude.

CANAL ZONE: near Gorgona and Maumé, *Wagner, s. n.*; Darién, *MacBride 2703*. PANAMÁ: forests on dry limestone, around Alhajuela, Chagres Valley, *Pittier 2398*; vicinity of Pacora, *Allen 1126, 2033*.

Rather near *Nectandra Gentlei*, a widespread species in Central America, but separated by the narrowly elliptic or elliptic-lanceolate leaf-blades and the yellowish lateral nerves diverging from the costa at an angle of 25–35 (–45)° and usually bearing large ellipsoid pubescent axillary glands on the lower surface.

4. Nectandra Laurel Klotzsch & Karsten ex Nees, in Linnaea 21:505. 1848.

Tree to 16 m. high; branchlets thick, densely ferruginous-tomentose becoming grayish, somewhat angled. Leaves alternate, occasionally near the tips of the branchlets becoming opposite or subopposite; petioles 1.5 (–2.5) cm. long; blades usually ferruginous-tomentose throughout, quickly becoming glabrous above except for venation, greenish brown when dried, coriaceous, elliptic or ovate, (6–) 10–15 (–35) cm. long and 3–6 (–15) cm. broad, the base obtuse usually, the apex obscurely or sharply acuminate, the acumen often to 2.5 cm. long, penninerved, ferruginous-pubescent throughout, impressed above, elevated beneath, the nerves 7–9 (–14) pairs, impressed above, elevated beneath, diverging from the costa at an angle of 35–45°, the transverse venation impressed above, prominent beneath. Inflorescence axillary or often subterminal, paniculate, 8 (–20) cm. long, densely ferruginous-tomentose, few- to many-flowered, the peduncles 5–7 cm. long. Flowers to 15 mm. in diameter, fragrant, the pedicels to 2 mm. long, the perianth white, pubescent, the lobes fleshy, pubescent, (5–) 7 mm. long; stamens of ser. I & II 1.7 mm. long, the anthers broadly ovate, obtuse, the connective tissue papillose, the filaments short and comparatively slender, those of ser. III to 1.7 mm. long, the filaments conspicuously biglandular; staminodia 0.3 mm. long; gynaecium glabrous, 2.3 mm. long, the ovary ovoid or obovoid, slightly larger than the style, the stigma obtuse, discoid. Fruit ellipsoid, smooth, to 12 mm. long

and 8 mm. in diameter; the cupule hemispherical, about ¼ the length of the entire fruit.

Andes of Peru as far north as Panama.

CANAL ZONE: without exact locality, *Hayes 1047.*

This species has two close relatives. The first is *Nectandra rigida,* from which it may be distinguished (See Kostermans in Meded. Bot. Mus. Utrecht 25:29. 1936) by its usually alternate leaves, which are elliptic or ovate, with an obtuse base, and are coriaceous with the nerves conspicuously impressed above. The leaves of *N. rigida,* however, are usually opposite, at least the upper ones, lanceolate, with acute bases, and rigidly coriaceous. The second affinity is seen in *N. reticulata,* which is at once distinguished by the presence of a basal auricle with reflexed margins. Kostermans (l. c.) has noted, also, the glabrous inner surface of the tube of *N. rigida,* as opposed to the densely sericeous hirsute tube of *N. reticulata.*

5. NECTANDRA RIGIDA Nees, Syst. Laurin. 284. 1836.

Shrub or medium-sized branching tree, to 15 m. high; branchlets densely ferruginous-tomentellous becoming glabrous, somewhat angled. Leaves opposite usually, at least the upper ones; petioles stout, ferruginous-tomentellous, becoming grayish, up to 2 cm. long; blades more or less glabrous at maturity, brown, shining above, pubescent and paler beneath, elliptic or lanceolate, 12–25 cm. long and 3.5 cm. broad, the base acute, occasionally obtusish, the apex acuminate, penninerved, the costa slightly elevated above, glabrous except at the base, conspicuously elevated beneath and pubescent, the nerves usually 8–10 pairs, rather inconspicuous above, elevated and pubescent beneath, arcuate, diverging from the costa at an angle of 45–55° (–75°), the transverse venation conspicuous beneath and pubescent. Inflorescence subterminal, axillary, paniculate, less than 5 cm. long, densely ferruginous-pubescent, many-flowered, the peduncle short. Flowers 9–10 (–14) mm. in diameter, the perianth white, ferruginous-tomentose without, the lobes broadly elliptic; stamens of ser. I & II 1.8 mm. long, sessile, the anthers ovate, the connective tissue papillose, those of ser. III 2 mm. long, conspicuously biglandular; staminodia small; gynaecium 2.3 mm. long, the ovary obovoid, slightly shorter than the style, the stigma triangular-discoid. Fruit ellipsoid, to 15 mm. long and 10 mm. in diameter, the cupule hemispherical, rugulose, less than ¼ the length of the entire fruit.

Tropical America from Panama to Brazil.

CANAL ZONE: Mindi, *Hayes 615;* in woods near Gatún, *Hayes 916.*

For discussion of relationships see the preceding species.

6. NECTANDRA GLOBOSA (Aublet) Mez in Jahrb. Bot. Gart. Berlin 5:415. 1889, excl. syn.

Laurus globosa Aubl. Pl. Guian. 1:364. 1775.

Tree 4.5–15 m., or shrub 3–6 m. high; branchlets closely and minutely sub-

ferruginous-pubescent, in the early stages angled and flattened at the nodes, later becoming reddish brown, striate, and glabrous. Leaves alternate; petioles stout, minutely pubescent to glabrous, canaliculate, to 1.5 cm. long; blades early minutely pubescent, becoming glabrescent to glabrous, coriaceous, usually shining above, dull beneath, elliptic to oblong-elliptic, 14–16 (–24) cm. long and 4–5 (–10) cm. broad, the base rounded or sharply cuneate, the latter appearance due to the lower half centimeter or so of the leaf-blade being recurved, the apex long-acuminate, penninerved, the costa slightly impressed above, rather conspicuous and elevated beneath, the nerves 8–12 pairs, inconspicuous above and elevated beneath, diverging from the costa at an angle of 30–45°, axillary pubescent glands frequently present, the reticulation obscure. Inflorescence axillary, rarely subterminal, paniculate, to 12–15 (–20) cm. long, minutely subferruginous-pubescent to glabrescent, many-flowered, stout, usually wide-branching, the peduncle variable, from extremely short to 8 cm. long. Flowers large and conspicuous, white, to 12 mm. in diameter, the perianth-lobes elliptic or obovate-elliptic, acutish or obtuse, the inner often more narrow than the outer, reflexed, very fleshy, papillose within, pubescent without, 4–5 mm. long; stamens of ser. I & II 1.25 (–1.5) mm. long, the anthers sessile or subsessile, rounded or broadly rounded-ovate, the fleshy papillose connective often one-third the entire length; those of ser. III to 1.7 mm. long, the anthers broad, narrowing slightly into the thick filaments almost one-

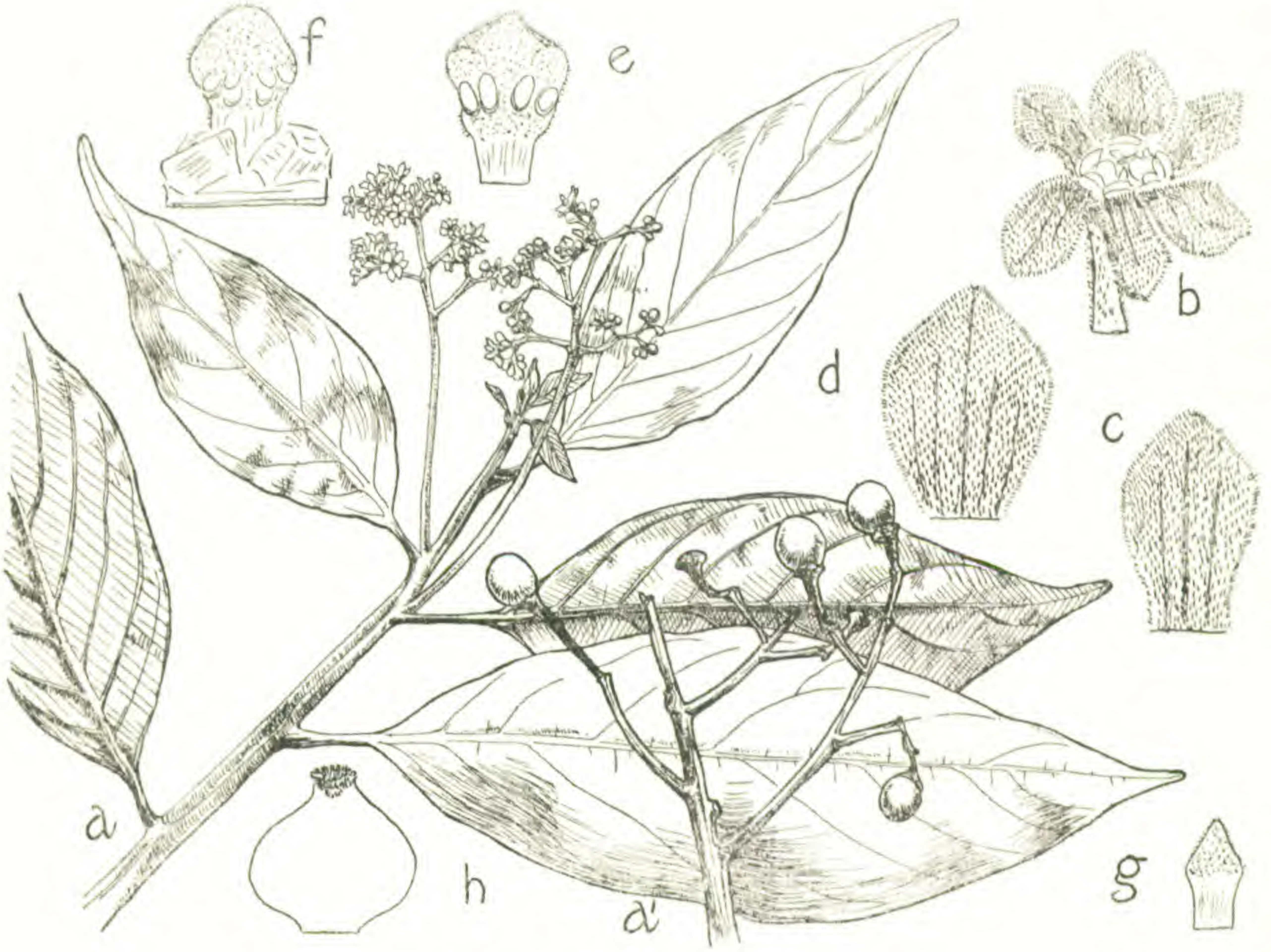

Fig. 27. *Nectandra globosa*

half their length, the glands conspicuous, spreading, sessile, almost the length of the anthers; staminodia triquetrous, to 1 mm. long, the thick stipe nearly one-half the entire length; gynaecium glabrous, to 1.7 mm. long, the ovary subglobose, two-thirds the entire length, the style short, the stigma subsessile, triangular-discoid or occasionally obtuse. Fruit globose, apiculate, about 1 cm. in diameter, the subtending cupule very shallow, up to 2 mm. long, 8 mm. in diameter and 2 mm. deep, the margin usually entire and thin, the pedicel to 5 mm. long, expanded to 3 mm. in diameter at the apex.

Widespread through the tropics of America, from the West Indies, Mexico and Central America, at varying altitudes. In Panama usually 10 to 100 meters along the coast; from 600 to 900 meters farther inland in the mountains. Known as "Sweetwood," *Sigua.*

BOCAS DEL TORO: Changuinola Valley, *Dunlap 215, Cooper & Slater 86 (Y 10267).* CHIRIQUÍ: San Felix, *Pittier 5145.* COCLÉ: above Penonomé, *Williams 257, 319, 530.* CANAL ZONE: without locality, *Hayes 1021, 1037, 1038;* Gatún Lake, near laboratory, *Wetmore & Abbe 17, 43, Woodworth & Vestal 314;* alluvial bottom near Bohio, *Maxon 4772;* vicinity of Miraflores Lake, *G. White 191, P. White 276;* between Miraflores and Corozal, *Pittier 2495;* near lake, vicinity of Cocoli River, *P. White 95;* Barro Colorado Island, *Brown 40, 68, 72, 188, Shattuck 314, 458, 807, Wilson 2;* along Río Fató, in forests or thickets, *Pittier 3873.* PANAMÁ: vicinity of Arraijan, *Allen 1622;* Chepo, *Kluge 27.* DARIÉN: Chepigana, Tucuti, *Terry & Terry 1391.*

This widespread species is very distinct, because of the large coriaceous leaves with obscure reticulation, the venation very prominent beneath, the base of the blade recurved for about a half-centimeter or so, and the large conspicuous white flowers developing into globose fruit.

7. NECTANDRA RAMONENSIS Standley in Field Mus. Publ. Bot. 18:453. 1937.

Tree 6–15 m. high; branchlets closely and minutely subferruginous-pubescent becoming grayish, outer cortex sometimes flaking off to reveal a dark reddish brown color. Leaves alternate; petioles short, slender, pubescent, less than 1 cm. long; blades sericeous beneath becoming minutely pubescent, often shining above, dull beneath, elliptic, occasionally oblong-elliptic, 7–11.5 cm. long and 2.5–6 cm. broad, the base obtuse and/or the lowermost portion attenuately cuneate, frequently recurved and almost decurrent, the apex obtuse to acutish or acuminate, penninerved, the costa slightly impressed above and somewhat obscure and slightly elevated beneath, the nerves not more than 4 or 5 (–7) pairs, slightly impressed above and somewhat obscure and slightly elevated beneath, diverging from the costa at an angle of 35–45°, the axillary glands pubescent. Inflorescence axillary or subterminal, paniculate, to 8 cm. long, comparatively few-flowered, minutely subferruginous-sericeous-tomentellous, the long peduncles stout, frequently up to 6 cm. long. Flowers large and conspicuous, to 15 mm. in diameter, the perianth-lobes elliptic or obovate-elliptic, acutish or obtuse, reflexed, very fleshy, papillose

Fig. 28. *Nectandra ramonensis*

within, pubescent without, 4–5 mm. long; stamens of ser. I & II 1.25 (–1.5) mm. long, the anthers sessile or subsessile, rounded or broadly rounded-ovate, the fleshy papillose connective often one-third the entire length; those of ser. III 1.7 mm. long, the anthers broad, narrowing slightly into the thick filaments almost one-half their length, glands conspicuous, spreading, sessile, almost the length of the anthers; staminodia triquetrous, to 1 mm. long, the thick stipe nearly one-half the entire length; gynaecium glabrous, 1.7 mm. long, the ovary subglobose, two-thirds the entire length, the style short, the stigma triangular, discoid or obtuse, frequently decurrent. Fruit ellipsoid, 1.5 × 9 mm., the subtending cupule 4–5 mm. long, 8–10 mm. in diameter and 2–3 mm. deep, the pedicel about 5 mm. long, and 3–4 mm. in diameter at the apex.

Costa Rica and adjacent Panama, at an altitude of 600 to 1140 meters.

CHIRIQUÍ: Boquete, *Davidson 566*. COCLÉ: vicinity of El Valle, *Allen 1635*; north rim of El Valle, *Alston 1858*.

Very close to *Nectandra globosa*, but with smaller leaves, the inflorescence fewer-flowered, and the fruits ellipsoid.

8. Nectandra Gentlei Lundell in Contr. Univ. Mich. Herb. 6:13. 1941.

Tree? 3–20 m. high; branchlets closely and shortly subtomentellous-pubescent, becoming pale ferruginous or brownish, presently fuscous, and eventually glabrescent to glabrous, dark reddish brown and striate. Leaves alternate or occasionally

Fig. 29. *Nectandra Gentlei*

subopposite; petioles canaliculate, brown-tomentellous, to 1.5 cm. long; blades early sericeous throughout, soon becoming glabrescent to glabrous above, remaining shortly but persistently pubescent beneath, chartaceous, lanceolate, to 20 cm. long and to 4.5 (–5) cm. broad, the broadest part of the blade being at or below the middle, the base seemingly cuneate, actually rounded or even subauriculate, the extreme bases usually tightly recurved, the apex attenuate into a slender acumen which may or may not be caudate, penninerved, the costa slightly impressed and rather inconspicuous above, prominently elevated beneath, the lateral nerves 4–6 pairs, occasionally 7 or 8, slightly impressed and rather inconspicuous above, prominently elevated beneath, diverging from the costa at an angle of about 45°, at a distance of about 1–1.5 cm. from their origin ascending abruptly to follow the outline of the leaf-blade almost parallel with the midrib. Inflorescence axillary, paniculate, to 8 (–12) cm. long, subferruginous- or brown-tomentellous becoming glabrescent, the peduncle (2–) 4 (–6) cm. long. Flowers to 3 mm. long and 5.5 mm. in diameter, the perianth yellow or white, sometimes fragrant, the tube well defined, constricted at the apex, and about 1 mm. long; the lobes usually elliptic, rather thick and papillose at the tip, 1.7 (–2.15) mm. long; stamens of ser. I & II 0.6–0.8 mm. long, the anthers subreniform-globose, almost sessile; those of ser. III 0.8 (–1.25) mm. long, the anthers almost square, slightly emarginate, the large conspicuous basal glands frequently contiguous; staminodia variable,

lanceolate, oblanceolate, or even ovate, slender, stipitate, often pubescent; gynaecium glabrous, 1.7 mm. or less long, the ovary ovoid, slightly shorter than the style, the stigma conspicuous, triangular, slightly decurrent. Fruit black at maturity, subglobose, about 8 mm. in diameter (or elliptic, 9 × 6–7 mm.), the subtending cupule thin, shallow, not more than 3 mm. long, 6 mm. in diameter, and usually less than 2 mm. deep, glabrous, with an entire margin, the pedicel less than 5 mm. long and expanded at the apex to about 2 mm. in diameter.

Southern Mexico through Guatemala, Honduras, and British Honduras to Panama, at low altitudes for the most part, although possibly it occurs as high as 900 and 2000 meters in Coclé and Darién.

CHIRIQUÍ: El Pedregal de David, *Pittier 5117;* vicinity of San Felix, *Allen 3650.* COCLÉ: Bismark, above Penonomé, *Williams 617.* CANAL ZONE: vicinity of Miraflores Lake, *P. White 243;* Ancon Hill, *Killip 3032, Standley 26376;* near Quarantine Station, *Pittier 2076;* hospital grounds at Ancon, *Pittier 2733;* between Corozal and Ancon, *Pittier 2639;* Balboa, hillside, west of Canal, *Rowlee & Stork 987.* PANAMÁ: San José Island, Perlas Archipelago, Gulf of Panama, *Johnston 82, 221, 270, 521, 699, 716.* DARIÉN: Cana and vicinity, *Williams 797.*

Distinctive because of the narrow lanceolate leaf-blades, with the extreme bases recurved, and the apices attenuate into a slender acumen which may or may not be caudate. Very near *Nectandra Pichurim* from South America, but differs in a more shallow cupule. Similar also to the South American *N. cuspidata,* but separable on foliage as well as floral characters.

9. NECTANDRA WOODSONIANA C. K. Allen in Jour. Arnold Arb. 26:380. 1945.

Tree 7–15 m. high; branchlets shortly appressed fulvous-tomentellous, becoming glabrescent, brunnescent, finally angled, striate, glabrous, gray. Leaves alternate; petioles more or less blackish, canaliculate, pubescent or glabrescent, to 1.5 (–2) mm. long; blades glabrescent or glabrous, except for axillary glands, in the dried state gray-green, elliptic or oblong-elliptic, to 24 cm. long and 8 cm. broad, the base cuneate, the apex obtuse, acute or acuminate, penninerved, the costa conspicuous above and slightly impressed, beneath elevated, the nerves 7 or 8 (–10) pairs, slightly elevated above, strongly beneath, diverging from the costa at an angle of about 35–45°, the reticulation conspicuously elevated throughout. Inflorescence axillary or subterminal, paniculate, to 20 cm. long, densely and appressed gray-pubescent becoming glabrescent, many-flowered, the peduncle to 10 cm. long. Flowers to 3 mm. long, the pedicels 2–3 mm. long, pubescent, the perianth white, the lobes thick, fleshy, papillose within, pubescent without, elliptic or ovate or narrowly obovate, to 2.5 mm. long; stamens of ser. I & II 0.6–0.8 mm. long, the anthers subreniform, twice the length of the stout filaments; those of ser. III 0.9–1.25 mm. long, the anthers quadrate, equaling the filaments; staminodia ovate, obtuse or subtriquetrous, 0.5 mm. long, the stout stipe nearly one-half the entire length; gynaecium glabrous, to 1.7 mm. long, the ovary ovoid, equaling three-quarters the entire length, the style short, the stigma triangular-discoid, conspicuous. Fruit reddish black in the dried state, ellipsoid, to 16 × 11 mm.,

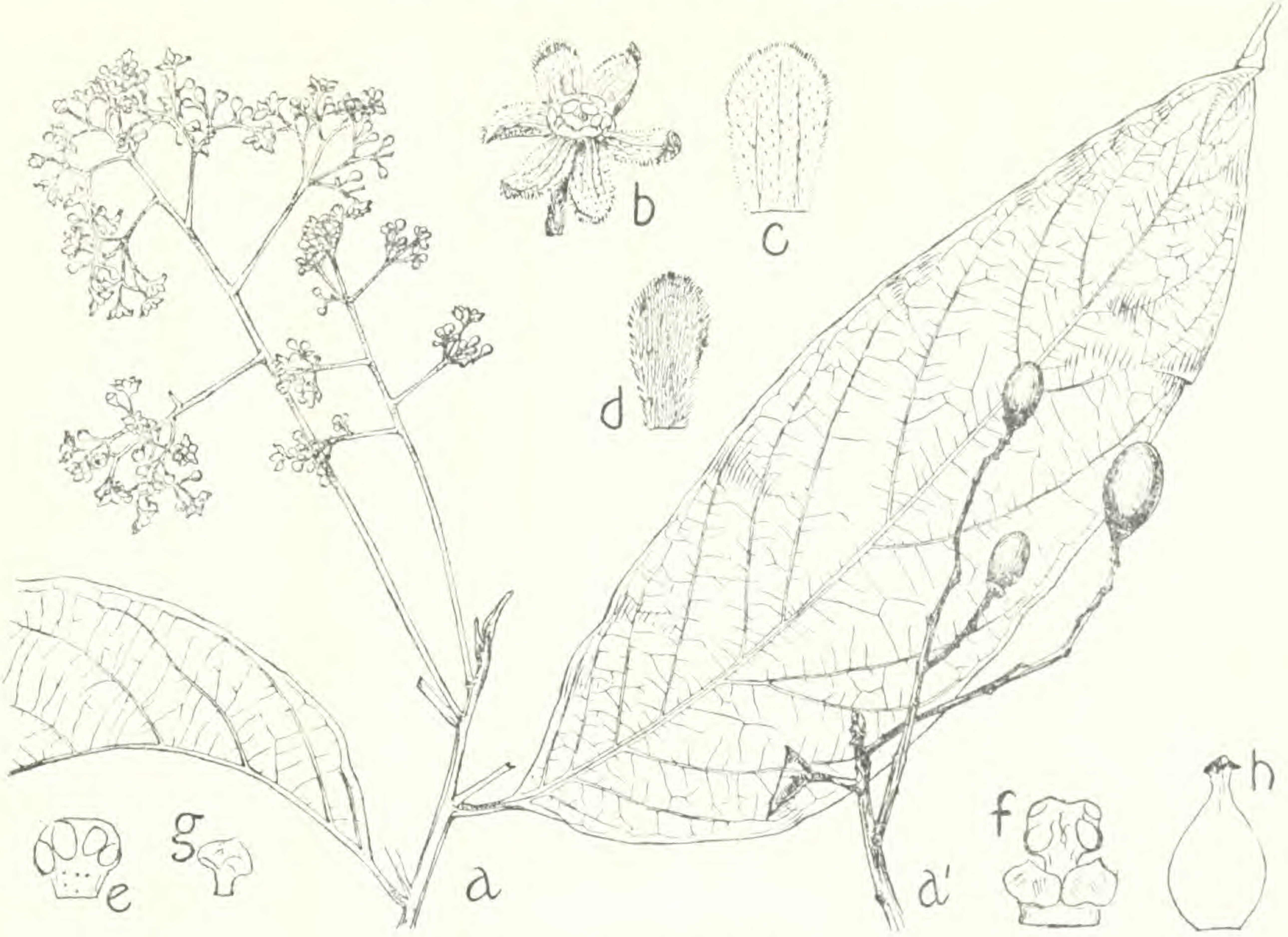

Fig. 30. *Nectandra Woodsoniana*

the subtending cupule shallow, discoid, ligneous, glabrous or glabrescent, rugulose, to 2 mm. long, 5–6 mm. in diameter, and 1 mm. deep, the enlarged pedicel striate, glabrescent, to 2 mm. long.

El Salvador, Costa Rica, at 1800 meters altitude, south at successively lower altitudes, finally occurring in Central Panama as low as 20 to 90 meters.

CANAL ZONE: Mamei Hill, *Pittier 3803;* vicinity of Salamanca Hydrographic Station, Río Pequení, *Woodson, Allen & Seibert 1620.* DARIÉN: Río Chico, vicinity of Yaviza, *Allen 4850.*

The species at once attracts attention because of the gray-green foliage and long grayish-pubescent inflorescence. Similar to *Nectandra martinicensis* from the West Indies, but the leaf-blades of the latter are smaller, and the margins recurved. Floral differences are apparent also.

10. NECTANDRA SALICINA C. K. Allen in Jour. Arnold Arb. 26:385. 1945.

Tree 5–8 m. high; branches densely foliose, gray, sulcate, glabrous; branchlets brown, presently gray, striate, angled. Leaves alternate; petioles slightly winged, slender, glabrous, canaliculate, 5–10 mm. long; blades glabrous throughout, shining above, less so beneath, coriaceous, in the dried state green or sometimes brown, slightly paler beneath, lanceolate, to 10 (–11) cm. long and 2–2.5 (–3.4) cm. broad, the base attenuately cuneate, the apex acute or attenuately acuminate, often attenuately obtusely acuminate, penninerved, the costa obscure above, conspicuously elevated beneath, the nerves 6 or 7 pairs, rather obscure throughout, diverging

Fig. 31. *Nectandra salicina*

from the costa at an angle of 25–35°, the reticulation sometimes conspicuous throughout, sometimes inconspicuous above. Inflorescence axillary, paniculate, 8–9 (–12) cm. long, glabrous, few-flowered, slender, the peduncle glabrous, 6–8 cm. long. Flowers to 3 mm. long, the pedicels slender, to 5 mm. long, the perianth shallowly subcampanulate, white (or sometimes pinkish or yellowish), the lobes oblong, recurved, thick, densely papillose-tomentose within and at the apex without, to 3 mm. long; stamens of ser. I & II 0.9 mm. long and broad, the anthers subreniform, frequently twice the length of the pubescent filaments, those of ser. III to 1.25 mm. long, the glands almost equaling the anthers; staminodia conspicuous, triangular or ovate, stipitate, 0.6 mm. or more long; gynaecium glabrous, 1.5 mm. long, the ovary subglobose, twice the length of the style, the stigma frequently triangular, conspicuous. Fruit green according to the collector, subglobose, apiculate, 20 × 18 mm., the subtending cupule red, minutely verruculose according to the collector, glabrous, to 6 mm. long, 10–12 mm. in diameter, and 2–3 mm. deep, the margin undulate, the pedicel enlarged, glabrous in the dried state, aciculate, to 1 cm. long.

Found at varying altitudes in Costa Rica, 850 to 1000 meters in Alajuela, 500 to 600 meters in Guanacaste, and in the cloud-forests of Panama, at 1980 meters. Known there as *Sigua blanca*, and used as firewood.

CHIRIQUÍ: Cerro Horqueta, Boquete, *von Hagen & von Hagen 2118*.

As far as may be ascertained from the description of the latter, *Nectandra salicina* is related to *N. nervosa*, but may be separated by the smaller leaves, shining above with usually conspicuous reticulation, the paniculate inflorescence, the subglobose, smaller fruits.

11. NECTANDRA FUSCOBARBATA (Mez) C. K. Allen in Jour. Arnold Arb. 26:390. 1945.

Nectandra glabrescens var. *fuscobarbata* Mez in Jahrb. Bot. Gart. Berlin 5:425. 1889.

Tree 6–12 m. high; branchlets brown, minutely sparsely pubescent, becoming gray, glabrous, striate. Leaves alternate, early sparsely pubescent becoming glabrescent and finally glabrous; petioles slender, canaliculate, sparsely pubescent above, to 1 cm. long; blades glabrous throughout except at the base of the costa beneath, membranaceous, in the dried state brown or greenish brown, lanceolate-elliptic, to 15 cm. long and 5 cm. broad, the base very attenuately cuneate, the apex longly caudate-acuminate, penninerved, the costa slightly elevated above, conspicuously so beneath, the nerves 4 or 5 (–8) pairs, more or less obscure throughout, diverging from the costa at an angle of 55°, the glands inconspicuous, the reticulation slightly prominulous throughout. Inflorescence axillary, loosely paniculate, to 15 cm. long, sparsely pubescent, the peduncle brown, sparsely pubescent, to 5 cm. long. Flowers to 3 mm. long, the slender pubescent pedicels

Fig. 32. *Nectandra fuscobarbata*

to 3 mm. long, the perianth campanulate, white or pale greenish, the lobes reflexed, papillose-pubescent, oblong, 2.5 mm. long; stamens of ser. I & II 0.6 mm. long, the anthers subreniform, two-thirds the length of the slender filaments which are pubescent at the base; those of ser. III 1 mm. long, the anthers oblong, equaling the filaments, the glands conspicuous, stipitate; staminodia usually ovate, stipitate, pubescent at the base, 0.6 mm. long; gynaecium glabrous, 1.25 mm. long, the ovary ovoid-globose, the style very short, the stigma capitate, conspicuous. Fruit abnormal (?), subglobose, apiculate, conspicuously gray-sericeous, minutely papillose, 7 mm. in diameter, subtending cupule shallow, glabrous, minutely verruculose, subcampanulate, 3 mm. long and 5 mm. in diameter, the pedicel to 5 mm. long, expanded to 3 mm. in diameter at the apex.

Described originally from the Isthmus of Panama, and found subsequently only in Panama along the coast at fairly low altitudes. Known as "Rock Sweetwood," and said to have a faint pleasant odor when fresh.

BOCAS DEL TORO: Fish Creek Hill, vicinity of Chiriquí Lagoon, *von Wedel 2431;* Isla Colon, *von Wedel 2866, 2969;* Flat Rock, region of Almirante, *Cooper 551 (Y 12184).*

Seemingly a cognate of *Nectandra salicifolia*, which does not occur in Panama, with similar floral structure except for pubescence of filament-bases and stipes of staminodia. More extensive collections may show that this is a geographical variation of the species proper.

12. NECTANDRA NITIDA Mez in Jahrb. Bot. Gart. Berlin 5:461. 1889.

Tree 13–15 m. high; young branchlets densely golden-"glittering"-tomentose, becoming gray, glabrous, terete. Leaves sparse; petioles canaliculate, to 6 mm. long; blades early sericeous-lanuginose, golden-"glittering" throughout, later glabrous throughout, chartaceous, varnished-shining above, opaque or subopaque beneath, ovate or elliptic, 12.5 cm. long and 5.5 cm. broad, the base acute, the apex acuminate, the margin minutely recurved, penninerved, the nerves immersed above, beneath prominently elevated, diverging from the costa at an angle of 25–45°, the reticulation very obscure and loose. Inflorescence subcorymbose, paniculate, shorter than the leaves, rather many-flowered, tomentose, the pedicels 2–5 mm. long, the bracteoles deciduous. Flowers to 5 mm. in diameter, the perianth yellow-tomentose, the lobes broadly elliptic-ovate, somewhat obtusely acute; anthers depressed, broader than long, the apex broadly truncate; the filaments of ser. I & II pilose; those of ser. III with large, conspicuous, sessile glands; staminodia small, thick, stipe-like; ovary glabrous, globose, 3–4 times shorter than the style; stigma obtuse. Fruit subglobose, 6 mm. long, mucronulate, with the rudiment of the style, the subtending cupule pateriform, smooth at the base, the margin entire, the pedicel one-third to one-quarter the entire length.

Reported from western Mexico at an unknown locality from the Haenke collection; and in Panama near Barbacans Station, S. *Hayes 133*.

Except for the original description, this species is unknown, or at least uncommented upon, by present-day workers in the family. It seems to be very close to

Nectandra latifolia, differing in leaf-blades that are prominently reticulated above and in the young stage scarcely sericeous beneath, the absence of axillary glands, branchlets that are sparkling "golden-tomentose," and buds that are golden-lanuginose. Authentic material is essential for further study.

13. Nectandra latifolia (H.B.K.) Mez in Jahrb. Bot. Gart. Berlin 5:454. 1889.

Ocotea latifolia H.B.K. Nov. Gen. & Sp. 2:133 [169]. 1817.

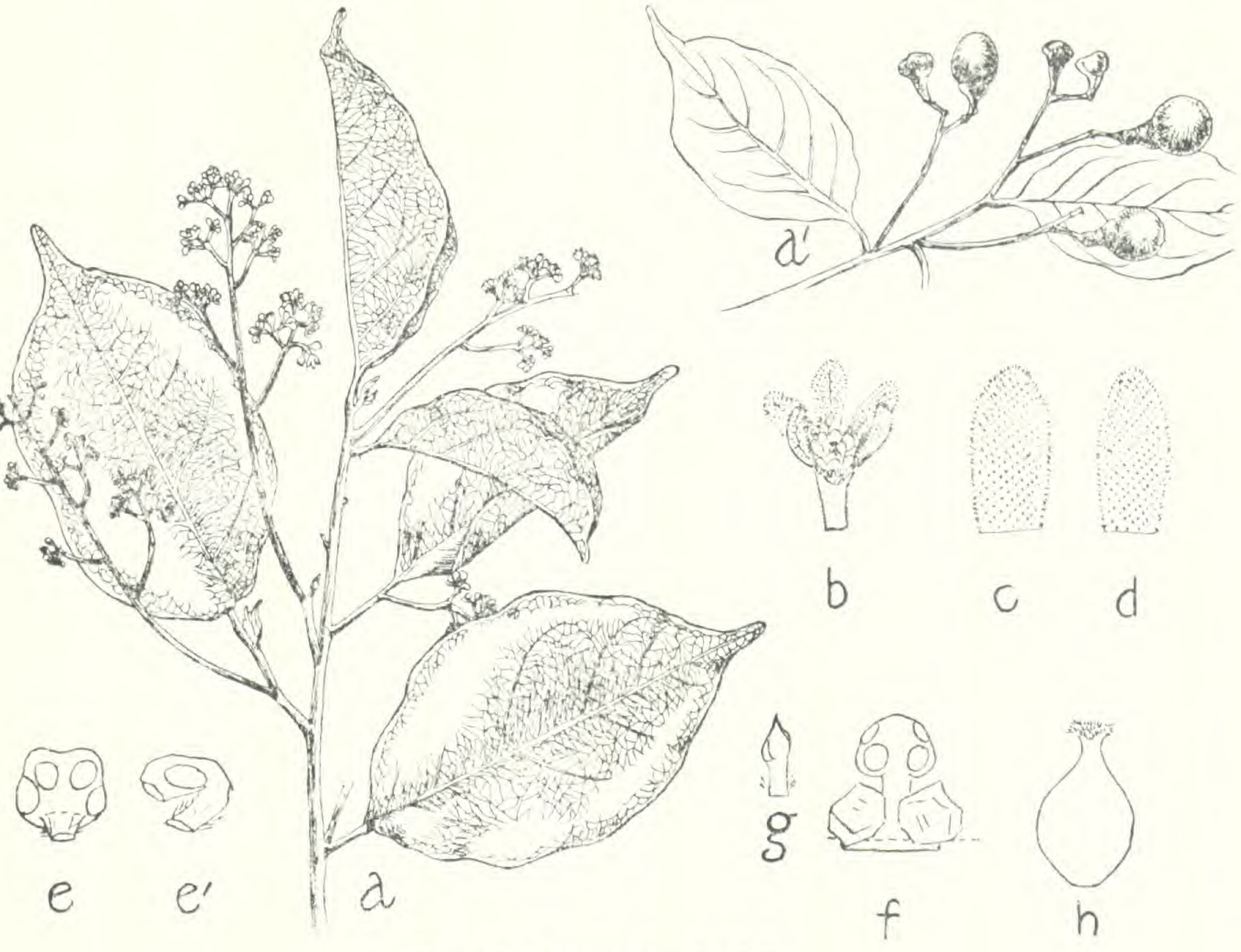

Fig. 33. *Nectandra latifolia*

Shrub or small tree to 8 m. high; branchlets early subferruginous- or yellowish-sericeous, becoming glabrous, reddish, striate. Leaves alternate or subopposite; petioles pubescent to glabrous, stout, usually canaliculate, 6–12 mm. long; blades becoming glabrous except for inconspicuous axillary glands, chartaceous to sub-coriaceous, very shining above, dull beneath, elliptic, 12 (–15) cm. long and 3.5 (–6.5) cm. broad, the base cuneate to roundish, the apex caudate-acuminate, penninerved, the costa and nerves somewhat obscure above and elevated beneath, the nerves 4–6 pairs, diverging from the costa at an angle of 35–50 (–55)°, the reticulation minute, exceedingly prominent above and beneath. Inflorescence axillary and subterminal, branching, subcorymbose-paniculate, to 9 (–13) cm. long, minutely pubescent, becoming glabrous, the peduncle to 5 cm. long. Flowers

to 6 mm. in diameter, the perianth-lobes thick, papillose, elliptic-ovate, 2.15–2.5 (–3.4) mm. long; stamens of ser. I & II 0.6–0.8 (–1) mm. long, the anthers more or less nutant, subreniform, slightly emarginate, twice the length of the rather stout filaments; those of ser. III 0.8 (–1) mm. long, the anthers squarish, about equaling the filaments, the glands conspicuous, sessile, nearly equaling the anthers; staminodia ovate, 0.6 mm. long, the stipes nearly one-half to two-thirds their entire length; gynaecium glabrous, 1.25 mm. long, the ovary subglobose or ellipsoid, nearly three times the length of the thick, short style, the stigma triangular-subcapitate. Fruit black, subglobose, about 1 cm. in diameter, the subtending cupule shallow, not more than 2 mm. long, 6 mm. in diameter, and 0.5 mm. deep, the margin slightly and finely undulate, the pedicel enlarged to 3–4 mm. long and 2.5 mm. in diameter at the apex.

Central America from Nicaragua through Panama, south through Colombia to Brazil, according to Mez. Occurring at low altitudes in Panama.

CANAL ZONE: without locality, *Christopherson 132;* hills near Gatún Station, Panama R. R., *Hayes 95, 98, 229, 483;* Gatún Lake, at turning point from canal, *Bangham 425;* Chagres, *Fendler 54;* Barro Colorado Island, *Aviles 113, 950, Bailey & Bailey 92, 307, Woodworth & Vestal 692.*

Outstanding because of the elliptic leaf-blades (reddish brown on drying) shining above and with minute reticulation exceedingly prominent above and beneath. See preceding species for discussion.

14. NECTANDRA STANDLEYI C. K. Allen in Jour. Arnold Arb. 26:396. 1945.

Tree 6–13 m. high; young branchlets minutely and densely fulvous- or sub-ferruginous-pubescent, angled, becoming glabrescent, striate, gray or blackish brown. Leaves alternate; petioles fairly stout, fulvous-tomentose, canaliculate, to 1.5 cm. long; blades minutely pubescent above, inconspicuously so beneath, coriaceous, in the dried state brown, elliptic, to 16 (–22) cm. long and 4.5 (–7) cm. broad, obtuse or almost rounded at the base, recurved and seemingly cuneate at the extreme base, the apex attenuately acuminate or caudate-acuminate, penninerved, the costa and nerves impressed above and conspicuously elevated beneath, the nerves 4 (–8) pairs, diverging from the costa at an angle of 25–35° (lowermost pairs sometimes to 55°), the reticulation obscure throughout. Inflorescence axillary or subterminal, paniculate, to 15 (–20) cm. long, fulvous- or gray-pubescent, many-flowered, the peduncle to 6 cm. long. Flowers to 3 mm. long, the pedicels pubescent, 2 mm. long, the perianth white, yellow, yellow-green or fulvous-flavescent according to the collector, campanulate, the lobes reflexed, fleshy, pubescent without, papillose within, elliptic, rounded, 1.7 (–2.15) mm. long; stamens of ser. I & II 0.6 mm. long, the anthers subreniform, subemarginate, subsessile; those of ser. III 1 mm. long, the anthers truncate, subemarginate, equaling the filaments, the glands laterally basal, conspicuous, subglobose, equaling the filaments; staminodia subovoid, 0.6 mm. long, the stipe nearly one-half the entire length; gynaecium glabrous, to 1.25 mm. long, the ovary ellipsoid, slightly longer

Fig. 34. *Nectandra Standleyi*

than the style, the stigma conspicuous, subtriangular, discoid. Fruit green according to the collector, subglobose, 1 (–1.3) cm. in diameter, the subtending cupule campanulate, glabrous, verrucose, the margin irregularly and shallowly lobed, 5–6 mm. long, 12 mm. in diameter, and 3 mm. high, the pedicel stout, verrucose, to 8 mm. long and expanded to 4–5 mm. in diameter at the apex.

Costa Rica from 250 to 1700 meters, and Panama presumably at low altitudes. Known as *Sigua*.

BOCAS DEL TORO: Cricamola, near Almirante, *Cooper 488;* vicinity of Chiriquí Lagoon, Big Bight, *von Wedel 2884;* Isla Colón, *von Wedel 2967.*

Similar to *Nectandra globosa* and *N. ramonensis* in foliage characters, but differing from the former in fewer pairs of lateral nerves and from the latter in larger leaf-blades, and from both species in its smaller flowers with anthers devoid of large papillose connective characteristic of the two above-mentioned species. The fruiting cupule of *N. Standleyi* is less shallow and the fruits tend to be subglobose.

15. NECTANDRA WHITEI (Woodson) C. K. Allen in Jour. Arnold Arb. 26:398. 1945.

Ocotea Whitei Woodson in Ann. Mo. Bot. Gard. 24:188. 1937.

Tree (6–) 20–30 m. high; branchlets slender, minutely and closely fulvous-sericeous, becoming glabrous, grayish and striate. Leaves alternate or subverticil-

Fig. 35. *Nectandra Whitei*

late; petioles slender, glabrous or glabrescent, and about 1 cm. long; blades early fulvous-sericeous, becoming glabrous above and less conspicuously pubescent beneath, coriaceous, oblanceolate, 12 cm. long and 3.5 (–4) cm. broad, the broadest portion above the middle of the blade, the base narrowly attenuate and recurved giving the appearance of a long winged petiole 3 cm. in length, the apex obtuse or obtusely and abruptly acuminate, penninerved, the costa slightly elevated above and more prominently so beneath, conspicuous throughout, the nerves 12 pairs, inconspicuous throughout, diverging from the costa at an angle of 35–45°. Inflorescence axillary or subterminal, paniculate, to 13 cm. long, the peduncle stout, reddish black, to 6 cm. long. Flowers about 3 mm. long, the pedicel slender, pubescent, not more than 3 mm. long, the perianth light greenish yellow, pubescent, the lobes rather thick, ovate-elliptic, subequal, 2.15 mm. long; stamens of ser. I & II 1 mm. long, the anthers subglobose, to twice the length of the stout filaments; those of ser. III 1.25–1.7 mm. long, the anthers squarish, almost equaled by the filaments, the glands subglobose, sessile, equaling the anthers; gynaecium glabrous, 2.15 mm. long, the ovary ovoid, slightly longer than the rather stout style, the stigma subtriangular, flat, decurrent. Fruit green becoming black, oblong or in the younger stages presumably ellipsoid, the surface frequently tuberculate, the apex in the dried state remaining conspicuously shining and unwrinkled, drying usually in a more or less regular star-shaped pattern, up to 4 × 1.5 cm., the subtending cupule cyathiform, red, verrucose, to 6 mm. long, 13 mm. in

diameter, and 2–3 mm. deep, the margin gently undulating, the pedicel verrucose, striate, up to 15 mm. long, and 6 mm. in diameter at the apex.

Western Panama and Costa Rica up to 2000 meters altitude. Known as *Bambito.*

CHIRIQUÍ: Valley of the upper Río Chiriquí Viejo, vicinity of Monte Lirio, *Seibert 307;* trail from Paso Ancho to Monte Lirio, *Allen 1486.*

Unique because of the long fruits. The species is near *Nectandra Paulii* from Costa Rica and Panama and *N. producta* from Costa Rica, but is distinguished from the former by shorter apparent petioles, and from the latter by its chartaceous leaf-blades, that are much smaller and with more prominent reticulation, and by its shorter inflorescences.

16. NECTANDRA HYPOGLAUCA Standley ex C. K. Allen in Jour. Arnold Arb. 26:399. 1945.

Tree 15–21 m. high; branchlets fulvous-sericeous becoming gray, striate, early angled, later terete. Leaves alternate; petioles stout, pubescent, apparently 2 (–2.5) cm. long, actually only 3.4 mm. long; blades glabrous above except at the base of the costa, shining, pubescent and glaucous beneath, coriaceous, in the dried state olive-brown, obovate-elliptic, to 18 cm. long and 8 cm. broad, the base attenuately cuneate, decurrent into the petiole, more or less strongly recurved through-

Fig. 36. *Nectandra hypoglauca*

out, making an apparent petiole, the apex rounded, slightly obtuse, or abruptly acuminate, penninerved, the costa slightly impressed above, rather elevated beneath, stout, the nerves 6–9 (or 10) pairs, scarcely elevated above, somewhat so beneath, more or less castaneous, diverging from the costa at an angle of 40°, the reticulation conspicuous throughout on the upper surface. Inflorescence axillary, paniculate, to 18 cm. long, bearing bracts in the early stages, densely fulvous-tomentose, the peduncles stout, striate, angled, to 8 cm. long. Flowers to 3.5 mm. long, the pedicels tomentose, to 4 mm. long, the perianth campanulate, densely fulvous-tomentose, canescent according to the collector, the lobes ovate, thick, obtuse, 2.5 mm. long; stamens of ser. I & II 1–1.25 mm. long, twice the length of the filaments, the anthers ovate, the connective one-third to one-half the length of the anthers; those of ser. III 1.25 (–1.7) mm. long, the anthers oblong, truncate, twice the length of the glands and filaments; staminodia broadly lanceolate, 0.8 mm. long; gynaecium glabrous, 1.7 (–3) mm. long, the ovary ovoid-globose or ellipsoid, twice the length of the style, the stigma triangular-peltate, conspicuous. Fruit in the dried state yellowish brown-maculate, obovoid-elliptic, conspicuously and obtusely apiculate, 2.2–2.5 × 1.6–2 cm., the subtending cupule campanulate, rugose, verrucose, glabrous, the margin slightly undulate, to 1 cm. long, 1.7 cm. in diameter and 5 mm. deep, the pedicel expanding to 15 mm. long and 5 mm. broad at the apex.

Known only from the rain-forests of Chiriquí, Panama, at 1340 meters altitude.

CHIRIQUÍ: Bajo Mona, Boquete, *Davidson 531*.

Outstanding for the robust branchlets and inflorescence covered with a fine but dense fulvous persistent tomentum, and the large coriaceous leaves that are shining above and glaucous-pubescent beneath.

17. Nectandra Paulii C. K. Allen in Jour. Arnold Arb. 26:400. 1945.

Tree to 30 m. high; branchlets stout, sulcate, minutely fulvous-tomentose, becoming gray-pubescent or glabrescent. Leaves alternate or subopposite, early sparsely and minutely appressed fulvous-pubescent becoming glabrescent, and eventually glabrous; petioles stout, pubescent, shallowly canaliculate, to 2 cm. long; blades glabrous above except for the base of the costa, below minutely pubescent, early membranaceous becoming coriaceous, in the dried state greenish brown, paler and subglaucous beneath, elliptic or obovate-elliptic, to 15 cm. long and 7 cm. broad, the base cuneate, somewhat recurved, decurrent into the petiole, the apex acute, acuminate or rounded, rarely emarginate, the margin slightly recurved, penninerved, the costa stout, conspicuous above, beneath strongly elevated, the nerves (6 or) 7 or 8 (or 9) pairs, conspicuous above but slightly impressed, beneath elevated, diverging from the costa at an angle of 35–45°, the reticulation obscure throughout. Inflorescence axillary, broadly paniculate, to 30 cm. long, pubescent, many-flowered, the peduncle stout, pubescent, to 10 cm. long. Flowers to 3 mm. long, the pedicel slender, 1–3 mm. long, the perianth hypocrateriform, white according to the collector, the lobes reflexed, thick, papillose-tomentose,

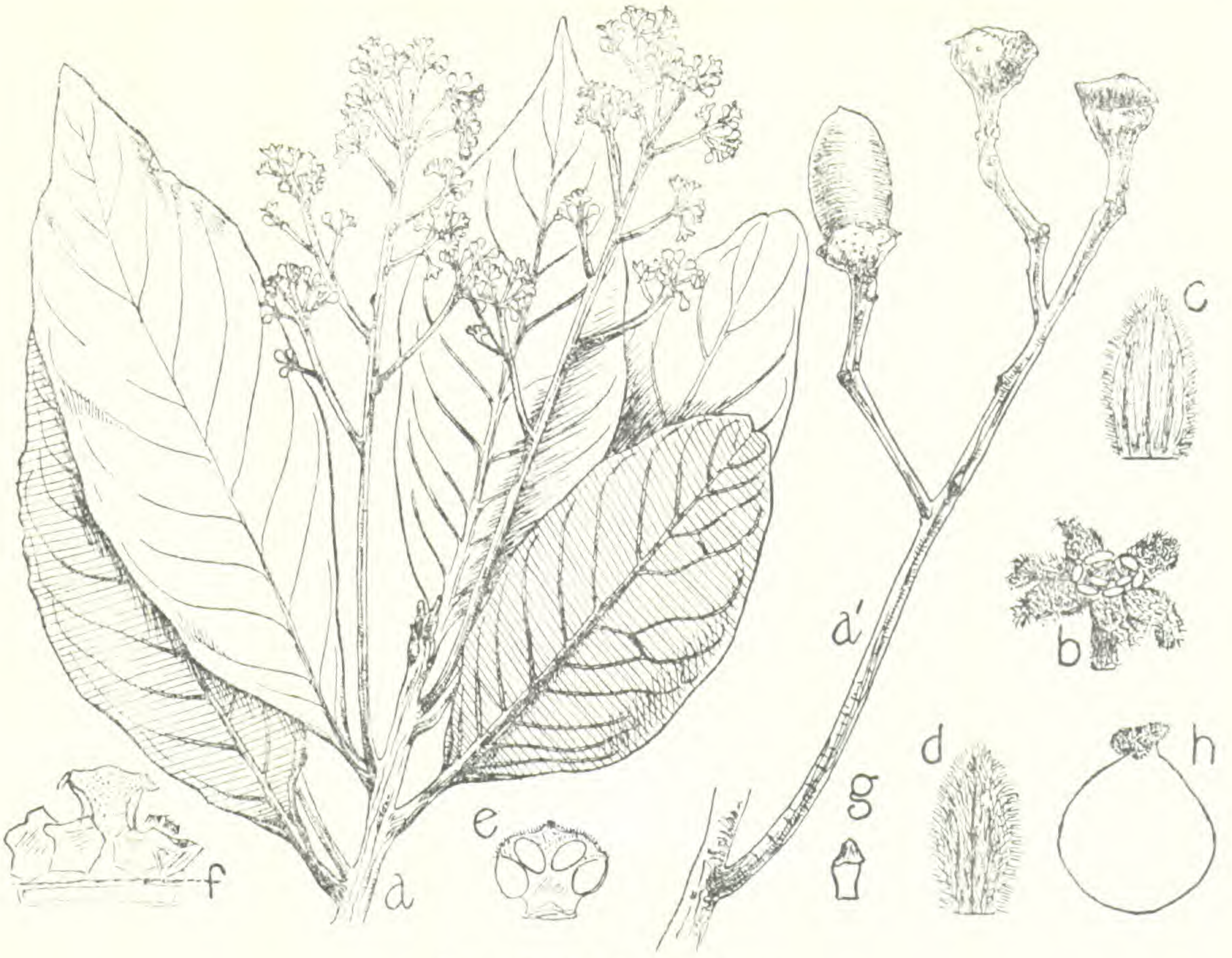

Fig. 37. *Nectandra Paulii*

oblong, 2.5–3 mm. long; stamens of ser. I & II 0.6 mm. long, the anthers subreniform or depressed-globose, twice the length of the filaments; those of ser. III 0.8 mm. long, the anthers quadrate and equaling the filaments, the glands also equaling the filaments; staminodia oblanceolate, pubescent, to 0.8 mm. long; gynaecium glabrous, 1.25 mm. long, the ovary subglobose, the style almost lacking, the stigma subsessile, rounded-triangular, conspicuous. Fruit ellipsoid, apiculate, 28 × 17 mm., the subtending cupule red, campanulate, thick, verrucose, glabrous, to 8 mm. long, 15 mm. in diameter, and 5 mm. deep, the pedicel pubescent, striate, enlarged to 1 cm. long, and 8 mm. in diameter at the apex.

Costa Rica up to 915 meters altitude, and Chiriquí at 1800–2000 meters altitude.

CHIRIQUÍ: Bajo Mona, mouth of Quebrada Chiquero, along Rio Caldera, *Woodson, Allen & Seibert 1022*; vicinity of Cerro Punta, *Allen 1572*.

Near *Nectandra hypoglauca*, but differences in floral as well as fruiting characters separate the two species.

18. NECTANDRA RETICULATA (Ruiz & Pavon) Mez in Jahrb. Bot. Gart. Berlin 5:404. 1889.

Laurus reticulata R. & P. Fl. Peruv. 4:*t. 348*, & Laurogr. *t. 23*. 1802.

Tree 6–12 (–24) m. high; branchlets densely conspicuously ferruginous-tomentose. Leaves alternate or subopposite; petioles stout, densely tomentose, to

Fig. 38. *Nectandra reticulata*

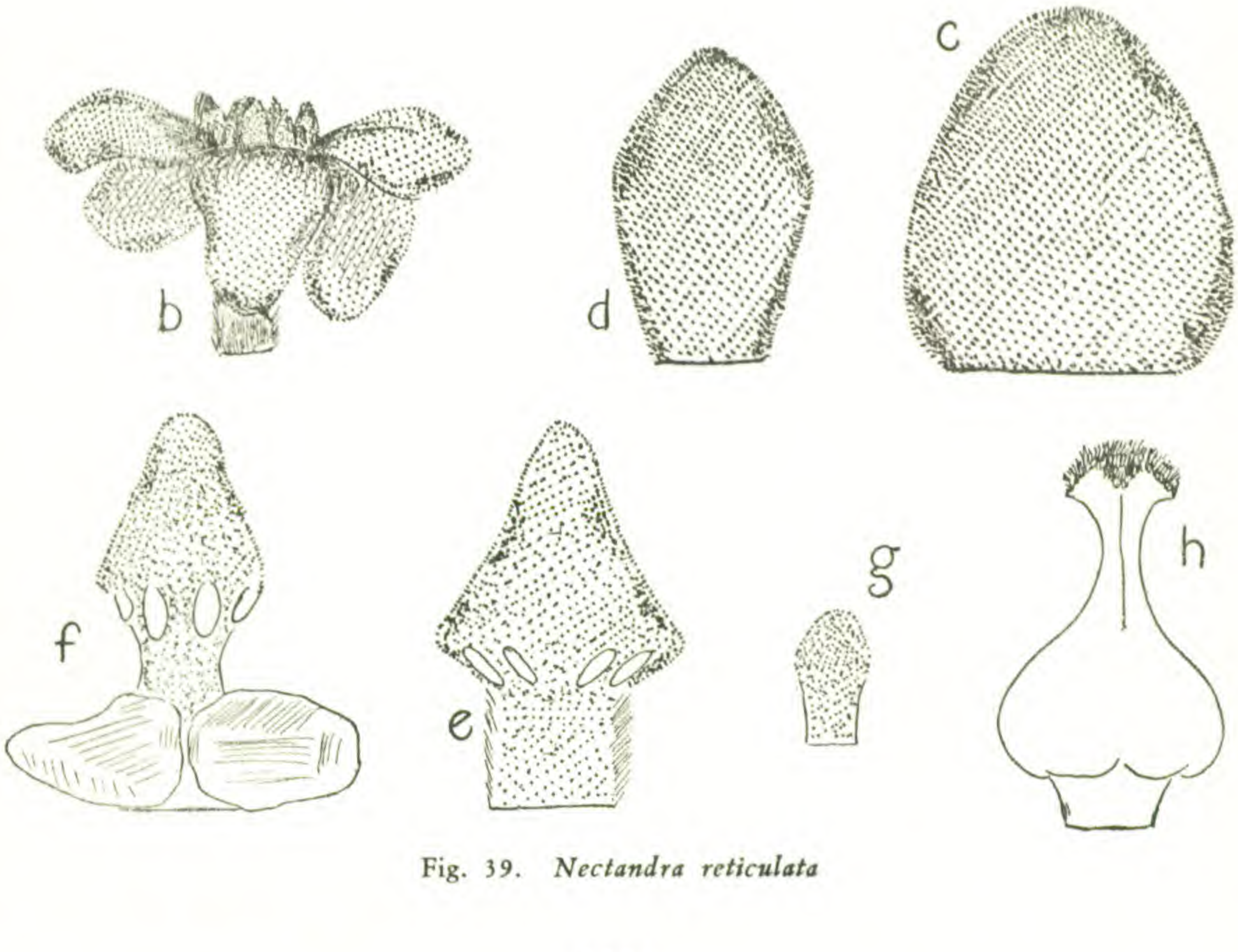

Fig. 39. *Nectandra reticulata*

1.5 cm. long; blades glabrous above except for the venation, coriaceous, lanceolate-elliptic or oblong-elliptic, to 30 cm. long and up to 10 cm. broad, the base auriculate and strongly recurved, the apex attenuate-acuminate, penninerved, the costa impressed and pubescent above, prominently elevated and densely pubescent beneath, the nerves up to 12 pairs, impressed and pubescent above, prominently elevated and densely pubescent beneath, diverging from the costa at an angle of 35–45°, the reticulation pronouncedly impressed above and conspicuously elevated beneath. Inflorescence axillary, paniculate, usually 10–20 cm. long, stout, many-flowered, ferruginous-tomentose, the peduncles up to 11 cm. long. Flowers large, 7 (–10) mm. long and 10–15 mm. in diameter, the pedicel usually 4–5 mm. long, often less, the perianth densely tomentose, the tube frequently densely hairy within, the lobes fleshy, tomentose-papillose within, ovate, obtuse or rounded, nearly 6 mm. long, the inner slightly shorter than the outer; stamens of ser. I & II often variable in size, to 2.4 (–3) mm. long, the anthers almost sessile, or with stout filaments one-third the entire length of the stamens, depressed-globose, to ovate and almost petaloid, the connective tissue occupying usually about one-half, often three-fourths, the entire anther; stamens of ser. III also variable, to 3 mm. long, the anthers often squarish and emarginate or occasionally ovate, the filaments sometimes almost equaling the anthers, the glands conspicuous, spreading, sessile, nearly equaling the anthers; staminodia ovate or linear-lanceolate, usually hairy, 0.8 mm. or more long; gynaecium for the most part densely pubescent, occasionally glabrescent or even glabrous (in Panama usually glabrous), 3 mm. long, the ovary ovoid or ellipsoid, slightly longer than the stout style, frequently with short broad stipe, the stigma conspicuous, subcapitate. Fruit said to be ellipsoid, to 13 mm. × 8 mm., the subtending cupule subpateriform, slender, simple-margined, one-third the entire length.

Originally described from Peru, but found throughout tropical America, from Mexico through Central to South America. Growing at consistently low altitudes in Panama. Known as "Sweetwood."

BOCAS DEL TORO: Changuinola Valley, Island Potrero, *Dunlap 22a;* Changuinola Valley, *Cooper & Slater 32 (Y 10132)*; region of Almirante, Cricamola, along river, *Cooper 512.* CANAL ZONE: forest along the Río Indio de Gatún, *Pittier 2775;* in swampy woods, Lion Hill Station, *Hayes 467;* Mindi, *Cowell 182.*

Easily the most striking and easily recognized species of Panama. Conspicuous for the densely ferruginous-tomentose branchlets, lower leaf-surfaces, and inflorescences. The blades are definitely strongly auriculate at the base and recurved to appear cuneate. The densely tomentose flowers are large, to 7 mm. long and 10–15 mm. in diameter.

5. BEILSCHMIEDIA Nees

Beilschmiedia Nees in Wallich, Pl. As. Rar. 2:61, 69. 1831.

Trees and shrubs. Leaves alternate or opposite, the blades penninerved, usually prominently and loosely reticulate above. Inflorescences axillary or subterminal, paniculate, short and few-flowered usually. Involucre none. Flowers perfect. Perianth-tube short, shallow, broadly obconical. Perianth-lobes subequal, or the outer shorter, deciduous. Stamens with filaments bearing anthers with two large cells; those of the outer series large, ovate, flattish, the connectives conspicuously protruding beyond the large introrse cells; stamens of the inner series with narrower, thicker anthers, with the connectives protruding beyond the lateral or extrorse-lateral cells, the filaments biglandular. Staminodia large, ovate-acute or triquetrous, shortly stalked or sessile. Gynaecium usually glabrous; ovary subglobose, short, merging into the thick short obtuse style. Stigma almost inconspicuous. Fruit usually ellipsoid, obtuse, outer layer thick or thin, usually fleshy, borne on a cylindrical, naked pedicel, scarcely elongated.

1. Beilschmiedia Austin-Smithii (Standley) C. K. Allen in Jour. Arnold Arb. 26:418. 1945.

Persea Austin-Smithii Standl. Field Mus. Publ. Bot. 18:1552. 1938.

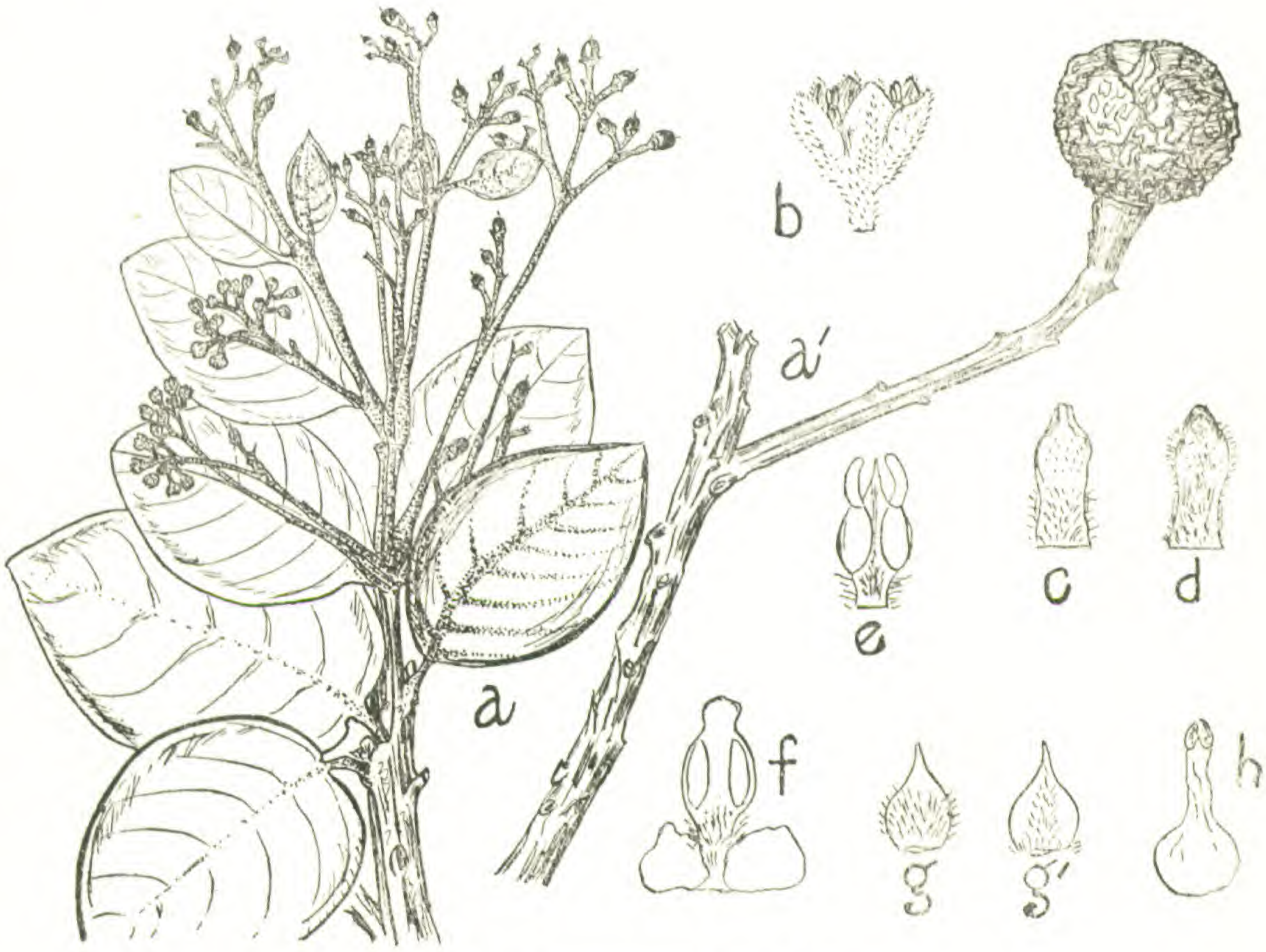

Fig. 40. *Beilschmiedia Austin-Smithii*

Tree to 30 m. high; branchlets densely foliose, the internodes very short, densely brownish-tomentose, angular or sulcate. Leaves alternate; petioles very thick, brownish-tomentose, to 1 cm. long; blades sparsely tomentellous, becoming almost glabrous above, beneath somewhat pubescent on the venation, rigidly coriaceous, brownish olive above, glaucous beneath, roundish ovate or suborbicular, 5.5–7 cm. long and 4.5–5 cm. broad, rounded at the base, often shortly and abruptly contracted into the petiole, the apex broadly rounded, penninerved, the costa somewhat thickened and elevated, the nerves 3–4 (–7) pairs, arcuate, diverging at an angle of 55–65°, the reticulation prominulous. Inflorescence axillary, paniculate, loosely sordid-tomentose, many-flowered, longer than the leaves, long-pedunculate. Flowers to 4.7 mm. long, the pedicels about 2 mm. long, thick, tomentellous; perianth dull yellow-brown, the lobes ovate, very obtuse, brownish-tomentellous without, about 2 mm. long; stamens of ser. I & II 1.5 mm. long, the anthers elliptic, narrowly truncate, twice the length of the broad pubescent filaments, the connectives protruding; those of ser. III 1.7 mm. long, the anthers ovate, truncate, the filaments bearing large glands that are fused; staminodia large, subcordate; gynaecium glabrous, to 1.7 mm. long, the ovary ovoid, topped by a very short style, the stigma obtuse. Fruit depressed-globose, 3.4 × 2.7 cm., the subtending pedicel enlarged to 1 cm. long and 1 cm. in diameter at the tip, 0.5 cm. in diameter at the base, glabrous, somewhat rugose.

Known only from Costa Rica and Chiriquí, at an altitude of 2000 meters.

CHIRIQUÍ: vicinity of Cerro Punta, *Allen 3490.*

6. AIOUEA Aublet

AIOUEA Aublet, Pl. Guian. 1:310, *t. 120.* 1775.

Evergreen trees or shrubs. Leaves alternate, occasionally verticillate, the blades obovate, usually yellowish green above, somewhat paler beneath, penninerved with more or less prominent nervation. Inflorescence of loose axillary pedunculate panicles. Bracts and bracteoles inconspicuous and early deciduous. Flowers small, perfect, usually subglobose or obconic, often with bloom. Perianth-tube shallow. Perianth-lobes approximately equal in size, and incurved. Stamens of all three series fertile (in Panama), with noticeable connective of varying length; anther-cells of two outer series introrse, and occupying almost the entire anther; two extrorse anther-cells of inner series, or four cells, the upper pair lateral and smaller than the lower extrorse pair; filaments of inner series conspicuously biglandular. Staminodia usually well developed, occasionally small and inconspicuous, but in Panama absent. Ovary glabrous. Style cylindrical and distinct from ovary or gradually increasing in diameter toward its junction with ovary. Stigma usually well developed and peltate, occasionally small and triangular. Fruit a berry, borne in a shallow, more or less fleshy cupule, the margin of which is plane, slightly undulate or (in Panama) bearing the remains of the six persistent and enlarged perianth-lobes.

The genus consists of thirty species, all but two of which occur in South America, the majority being native to Brazil. One species recorded from Costa Rica and the following species from Panama. Two of the South American species occur also in Trinidad. Timber used locally for construction and furniture.

1. Aiouea Lundelliana C. K. Allen in Jour. Arnold Arb. 26:419. 1945.

Tree 6–30 m. high; branchlets brownish gray, verruculose. Leaves alternate, verticillate, in early stages ferruginous-sericeous, presently glabrous; petioles thick-winged or decurrent, glabrous, canaliculate, to 2 cm. long; blades glabrous above, beneath slightly and obscurely pubescent, coriaceous, in dried state brown, obovate-elliptic, (12–) 16 (–18) cm. long and (5–) 7.5 cm. broad, the base attenuate-cuneate into the decurrent petiole and strongly recurved, the apex rounded or broadly acute or abruptly broadly and obtusely acuminate, rarely emarginate, the margin recurved, the costa scarcely elevated above, conspicuously and coarsely so beneath, the nerves 7 or 8 pairs, obscurely impressed above, elevated beneath, diverging from the costa at an angle of about 45°, the reticulation obscure above and prominulous beneath. Inflorescence broadly paniculate, up to 20 cm. long, glabrescent, many-flowered, long-pedunculate. Flowers up to 3 mm. long with equal pedicels; perianth subcampanulate, yellowish green, fragrant, the lobes more or less oblong or ovate, somewhat membranaceous, pubescent, ± 1.9 mm. long;

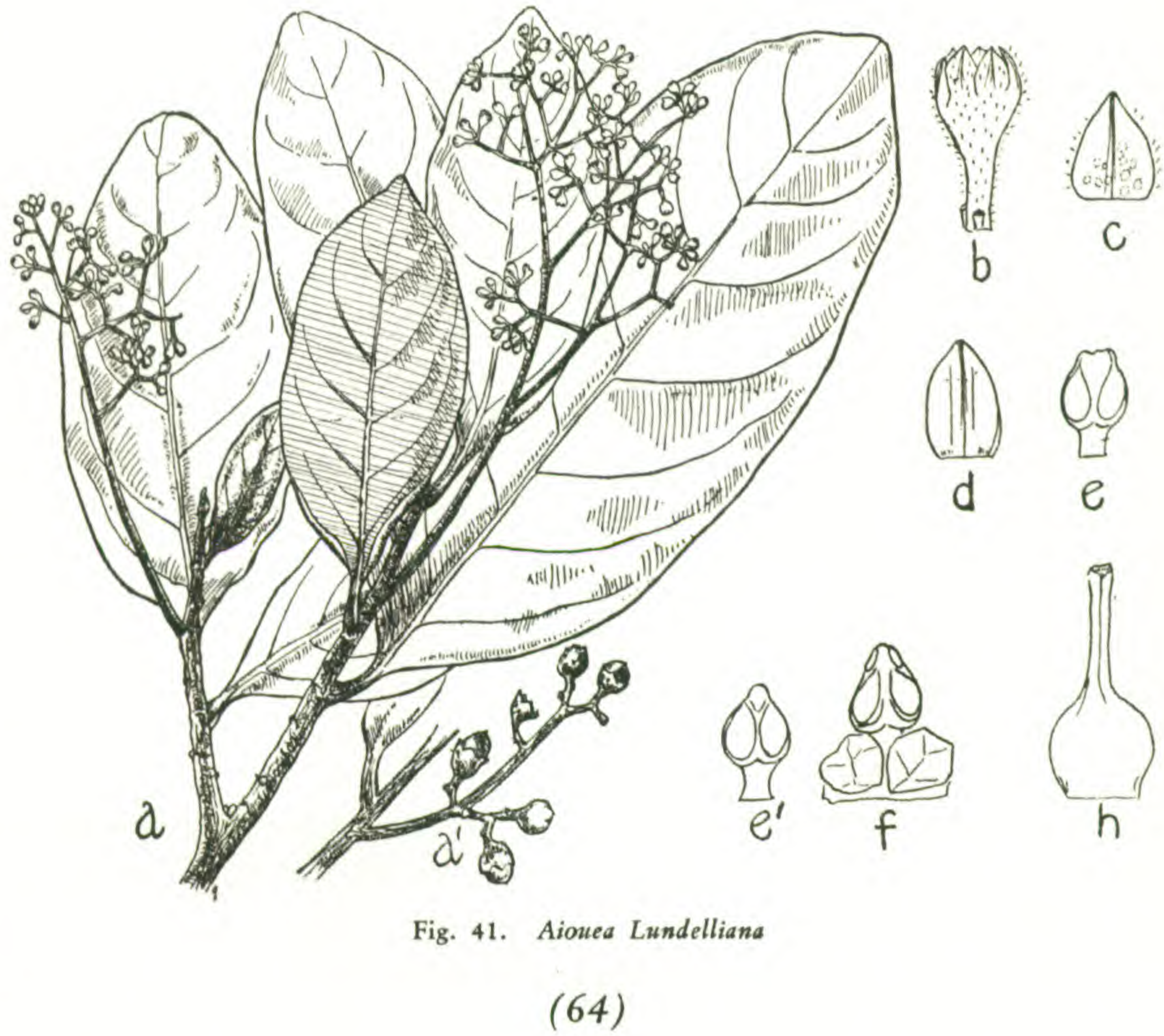

Fig. 41. *Aiouea Lundelliana*

stamens of ser. I & II ± 1.25 mm. long, the filaments shorter than or almost equaling the anthers; those of ser. III ± 1.7 mm. long, the anthers often slightly narrower and conspicuously biglandular, often 4-celled; staminodia none; gynaecium glabrous, ± 2.15 mm. long, the ovoid ovary equaling the style, the stigma small, inconspicuous. Fruit immature (?), green, oblong, 6 × 4 mm., the campanulate cupule more or less verruculose at the base, coarsely 6-toothed, glabrous, 6–7 mm. long, 6 mm. in diameter, and 3 mm. deep, the pedicel thickened, glabrous, 3 (–5) cm. long.

Known only from the rain-forests of eastern Panama, up to 2000 meters altitude.

CHIRIQUÍ: Río Chiriquí Viejo valley, near El Volcán, *P. White 225*; vicinity of Cerro Punta, *Allen 1570*; Bajo Chorro, Boquete, *Davidson 435*.

Differs from *Aiouea costaricensis* in having larger leaf-blades, abruptly, obtusely and shortly acuminate, with only slightly prominent reticulation beneath.

7. ENDLICHERIA Nees

ENDLICHERIA Nees in Linnaea 8:37. 1833 (non Presl).

Evergreen trees or shrubs. Leaves alternate and/or subverticillate, thinly chartaceous to rigidly coriaceous, penninerved, rarely subtriplinerved or subquintuplinerved, the lower surface often densely, microscopically puncticulate. Inflorescence axillary or subterminal, few- to many-flowered panicles. Bracts and bracteoles persistent or deciduous. Flowers dioecious, without involucre. Perianth-tube distinct, shallow to subglobose. Perianth-lobes 6, usually equal, mostly spreading and reflexed at anthesis. Staminate flowers with 9 fertile stamens in three series, the inner distant from the two outer. Anthers of outer stamens 2-celled, introrse or introrse-lateral, sessile or borne on filaments. Anthers of inner stamens usually 2-celled, extrorse or extrorse-lateral, the filaments biglandular. Staminodia generally absent, or if present very minute. Pistillate flowers usually smaller, and often borne on much shorter pedicels in usually shorter, more narrow panicles. Stamens similar, smaller and sterile. Ovary immersed in the tube, large, usually glabrous, but pubescent in Panamanian species. Style usually short and thick. Stigma discoid or peltate, distinct, varying in size, often 3-parted. Fruit usually ellipsoid, glabrous, borne in shallow subhemispherical fleshy simple-margined cupule, the pedicel enlarged, fleshy and thick.

The genus consists of forty species, one occurring in the West Indies and one in Panama, the rest in South America.

1. ENDLICHERIA BROWNIANA Mez in Jahrb. Bot. Gart. Berlin 5:115. 1889.

Oreodaphne glomerata Seemann, Bot. Voy. H. M. S. Herald, 193. 1854.
Aydendron macrophyllum Meissner in DC. Prodr. 15[1]:92. 1864.

Tree to 20 m. high; branchlets thick, subterete, minutely yellowish-appressed-tomentellous. Leaves alternate, early silvery-sericeous; petioles stout, obscurely

canaliculate, sulcate, densely sericeous-tomentellous, 1–2 cm. long; blades glabrous and shining above, beneath slightly sericeous, coriaceous, in the dried state green, broadly elliptic, 22–40 cm. long and 10–15 cm. broad, the apex somewhat obtuse or shortly acuminate, base acutish or somewhat obtuse, the costa very prominent, the lateral nerves 8 or 9 pairs, prominent, slightly arcuate, the reticulation coarsely prominent. Inflorescence axillary, few-flowered, sericeous-tomentellous, paniculate, up to 15 cm. long, the peduncles short, thick. Pistillate flowers 2.5–3 mm. long, the pedicels to 2 mm. long; perianth pink, pilose, the tube urceolate, 1.5 mm. long, slightly constricted at the apex, the inner surface sericeous-tomentellous; the lobes equal, erect-spreading, fleshy, somewhat flat, narrowly ovate, acutish, 1.5 mm. long, the inner surface tomentellous; stamens minute, 0.8 mm. long, well developed, substerile, the anthers ovate, acutish or truncate, the connective distinctly protruding beyond the small cells, the filaments very short, broad, densely pilose, those of ser. III biglandular; gynaecium pubescent, the ovary large, immersed in the perianth-tube, densely verruculose (sericeous-tomentellous), thickly ovoid, attenuate into a short style, the stigma distinct, discoid, subtriangular. Fruit unknown, the subtending cupule subhemispherical, rather smooth, to 11 mm. in diameter and 8 mm. high, merging into the obconical pedicel enlarged to 1 cm. in length.

Originally described from Seemann's collection from Cape Corrientes, then considered a part of the old province of Darién, Panama; now a part of modern Colombia. Presumably found at low altitudes along the sea-coast.

BOCAS DEL TORO: Fish Creek Mts., vicinity of Chiriquí Lagoon, *von Wedel 2257*.

8. LICARIA Aublet

LICARIA Aublet, Pl. Guian. 1:313, *t. 121.* 1775.

Misanteca Schlect. & Cham. in Linnaea 6:367. 1831.
Acrodiclidium Nees, Laur. Expos. 13. 1833.
Chanekia Lundell in Phytologia 1:177. 1937.

Evergreen trees or shrubs. Leaves usually alternate or occasionally opposite, the blades chartaceous or coriaceous, penninerved, usually somewhat thickened along the margin. Inflorescence usually of axillary and subterminal few- to many-flowered panicles. Involucre lacking. Flowers perfect. Perianth-tube usually distinct, occasionally short or even lacking. Perianth-lobes usually approximately equal. Stamens of ser. I & II small, only occasionally petaloid, and occasionally aborted, those of ser. III fertile, filamentous or sessile, usually biglandular, the anthers 2-celled, extrorse or apically extrorse. Staminodia usually absent. Ovary glabrous or sericeous, immersed in tube. Style slender. Stigma minute. Fruit first included in the enlarged tube, finally exserted, the base enclosed in a simple and thinly margined or thick and double-, rarely triple-margined cupule.

The genus consists of 48 recognized species, 32 of which are native to South America, 6 each from Mexico and Central America, including a single species from Panama, and 4 from West Indies. Timber good for general construction, but too scarce to be used to any great extent commercially.

1. Licaria excelsa Kostermans in Meded. Bot. Mus. Utrecht 42:595. 1937 (Rec. Trav. Bot. Néerl. 34:595. 1937).

Acrodiclidium excelsum Lundell in Amer. Midl. Nat. 19:428. 1938.

Large tree to 60 m. high, the trunk erect; branches gray, glabrous; branchlets thick, glabrous, with lenticels rather numerous, often somewhat shining, sulcate. Leaves alternate; petioles stout, glabrous, up to 23 mm. long; blades glabrous, rigidly coriaceous, almost shining, elliptic or subovate-elliptic, 20 (–24) cm. long and 5 (–8) cm. broad, the base shortly acute, the apex acuminate, the costa broad above, flattened beneath, prominulous and broadly flattened towards the base, the lateral nerves at least 10 pairs, filiform, prominulous above and beneath, erect-spreading, arcuate, the reticulation prominulous, very densely and minutely areolate. Inflorescence axillary and subterminal, paniculate, before anthesis densely ferruginous-sericeous-tomentellous, becoming glabrous. Infructescence stout, to 15 cm. long. Fruit ellipsoid-ovoid, glabrous, 2.5 × 2 cm., the subtending cupule almost hemispheric-cylindrical, conspicuously verruculose, 20 mm. long, 25 mm. in diameter, and 16 mm. deep, the margin obscurely double, the outer entire and

Fig. 42. *Licaria excelsa*

thickened, the inner extending less than 2 mm. above the outer, thinner, exhibiting a tendency to split at intervals towards the base, the pedicel enlarged to 15 mm. long and 10 mm. in diameter at the apex.

Panama and adjacent Costa Rica, in rain-forest. Known as *Siguatón.*

CHIRIQUÍ: southern slope of the mountain in moist forest, Cerro de la Horqueta, near castle of Las Siguas, *Pittier 3200;* rain-forest of Bajo Chorro, Boquete, *Davidson 361;* vicinity of Cerro Punta, *Allen 3482.*

Conspicuous because of the very large rigidly coriaceous leaf-blades, probably the largest to be found in the family in this area.

HERNANDIACEAE

Trees, usually with rather soft, white wood; leaves alternate, usually long-petiolate, simple or palmately lobed, occasionally with cystoliths or oil cells, and somewhat aromatic; flowers usually small, bisexual or unisexual, with a 2-seriate, undifferentiated or poorly differentiated, valvate perianth, borne in axillary or pseudoterminal, many-flowered panicles or thyrses; the staminate with 3–6 two-valved stamens frequently accompanied by glandular staminodia; the pistillate with a 1-celled, inferior ovary containing a single, pendulous ovule and rather fleshy stigma, frequently with glandular staminodia; fruit a drupe or 2-winged samara, the seed without endosperm.

Unlike the Lauraceae, to which they are related so closely, Hernandiaceae are very infrequent in tropical forests, usually found only as isolated specimens at rather low elevations. Besides *Hernandia,* the genera *Gyrocarpus* and *Sparattanthelium* are to be expected in Panama, since both are known to occur in Costa Rica and Colombia.

1. HERNANDIA L.

HERNANDIA L. Sp. Pl. 981. 1753; Pax in Engl. & Prantl, Nat. Pflanzenfam. 3^2:129. 1889.

Hertelia Neck. Elem. 2:345. 1790.
Hernandezia Hoffmsgg. Verz. Pflz. Nachtr. 1:219. 1824.
Biasolettia Presl, Rel. Haenk. 2:141. 1835.
Hernandiopsis Meissn. in DC. Prodr. 15:264. 1864.

Trees; leaves broad and long-petiolate, entire; flowers unisexual, borne in clusters of 2 staminate and 1 pistillate in sessile, involucrate cymules at the ends of the inflorescence branches; staminate flowers with 3 outer and 3 inner perianth lobes united at the base into a pedicel-like tube, containing 3 stamens and 3–6 glandular staminodia; pistillate flowers with 4 outer and 3 inner perianth lobes united at the base into a tube, the ovary enclosed within a more or less foliaceous cupule, the stigma fleshy, funiform, accompanied by 4 sessile, glandular staminodia inserted at the orifice of the perianth tube; fruit a nut, usually more or less 8-ribbed, enclosed within the greatly enlarged cupule.

Fig. 43. *Hernandia stenura*

a. Leaves ovate-oblong, broadly rounded at the base, not cordate, glabrous; pistillate cupule more than half as long as the perianth tube, rather thin in texture, the orifice obscurely and unequally 3-lobed, not involute.. 1. N. DIDYMANTHA

aa. Leaves broadly ovate, the base broadly cordate, more or less cinereous-puberulent beneath; pistillate cupule about one-third as long as the perianth tube, fleshy, truncate, the orifice margin strongly involute...... 2. N. STENURA

1. HERNANDIA DIDYMANTHA Donn. Sm. in Bot. Gaz. 31:120. 1901.

Trees 10–25 m. tall, buttresses absent or poorly developed; branchlets irregularly angulate, inconspicuously canescent to glabrous; leaves long-petiolate, the blade ovate-oblong, apex acutely acuminate, base broadly rounded, 15–30 cm. long, 6–15 cm. broad, membranaceous, glabrous when mature, the petioles 5–8 cm. long, glabrous; inflorescences about half as long as the subtending leaves, bearing several reduced, shortly petiolate leaves above, the ultimate branches terminating in involucrate cymules bearing 2 staminate and 1 pistillate, sessile or subsessile flowers; staminate flowers about 1 cm. long, densely canescent, the elliptic-oblong perianth lobes about equalling the tube, stamens 3, each subtended by paired, sessile staminodia, 4 mm. long, the anthers about as long as the filaments; pistillate flowers about 1 cm. long, densely canescent, the elliptic-oblong perianth-lobes about equaling the tube, the cupule more than half as long as the perianth-tube, somewhat longer than broad, rather thin in texture, the orifice obscurely and unequally 3-lobed, not involute. Mature fruit unknown.

Rain forest, northwestern Panama and adjacent Costa Rica.

BOCAS DEL TORO: Buena Vista Camp on Chiriqui Trail, alt. 1800 ft., Jan.-March, 1928, *Cooper 618*. CHIRIQUÍ: Progreso, 1927, *Cooper & Slater 220, 272.*

Cooper and Slater report that the trees of *H. didymantha* are not used for timber because the wood is light and soft, with a "woolly grain." Native names are *cebo macho* and *cebo burro.*

2. HERNANDIA STENURA Standl. in Field Mus. Publ. Bot. 18:1553. 1938.

Trees 7–15 m. tall; branchlets conspicuously angulate, minutely canescent to glabrate; leaves long-petiolate, the blade very broadly ovate, subcaudate-acuminate, broadly cordate, 12–30 cm. long, 6–20 cm. broad, membranaceous, minutely canescent to glabrate beneath, the petioles 7–12 cm. long; inflorescences about half as long as the subtending leaves, bearing several reduced, shortly petiolate leaves above, the ultimate branches terminating in canescent, involucrate cymules bearing 2 staminate and 1 pistillate, sessile or subsessile flowers; staminate flowers about 1 cm. long, densely canescent, the elliptic-oblong outer perianth lobes about equalling the tube, the stamens 3, each subtended by paired sessile staminodia, 4 mm. long, the anthers somewhat longer than the filaments; pistillate flowers about 1.2 cm. long, the perianth lobes about equalling the tube, the cupule about one-third as long as the perianth tube, about 2 mm. long and 4 mm. broad, fleshy, the orifice margin strongly involute. Mature fruit unknown.

Rain forest, northwestern Panama and adjacent Costa Rica.

BOCAS DEL TORO: Water Valley, November, 1940, *Wedel 1684, 2148.*

This species has been confused with the Antillean *H. sonora* L., which has smaller, obviously peltate leaves, and different floral structure. The wood of *H. stenura* is said to be very soft.

PAPAVERACEAE

Dicotyledonous annual, biennial, or perennial herbs (rarely woody), usually having a milky, yellow, or orange, acrid juice; leaves alternate, exstipulate, usually lobate or dissected; inflorescence ranging from solitary flowers to large, many-flowered compound panicles or cymes; flowers mostly polypetalous (apetalous in *Bocconia*), perfect, regular, hypogynous, frequently very large and showy; sepals 2 or 3, subvalvate or imbricate; petals 4–12, rarely absent, spreading, imbricate, frequently early caducous; stamens several to many, free; filaments filiform; anthers erect, bilocular, longitudinally dehiscent; ovary free, 2- to several-carpellate, usually 1-loculate (sometimes 2-loculate or imperfectly few- to several-loculate), 1- to many-ovulate; style short or obsolete; stigmas as many as the carpels, distinct or more or less adnate to the top of the ovary; fruit capsular, dehiscing by pores or valves, frequently containing an acrid or narcotic juice.

A relatively small family, chiefly of the northern temperate zones of both hemispheres, poorly and somewhat atypically represented in Panama and the tropics generally. The family contains many species of ornamental value, and also the opium poppy *(Papaver somniferum)* of considerable commercial and human significance.

Only two genera are indigenous to Panama, only one of which *(Bocconia)* is at all common. In addition, possibly a few species of ornamental poppy *(Papaver)* and the California poppy *(Eschscholtzia californica)* may occur under cultivation in the country. Both of these genera resemble *Argemone* but lack its prickly leaves. *Eschscholtzia* can be distinguished from *Papaver* by the linear capsule.

a. Unarmed trees or shrubs; flowers apetalous, the stigmas prominent; capsule 1-seeded .... 1. BOCCONIA
aa. More or less spiny herbs, rarely shrubs; flowers with conspicuous petals, the stigmas sessile; capsule many-seeded .... 2. ARGEMONE

1. BOCCONIA L.

BOCCONIA L. Sp. Pl. 505. 1753.

Small trees or shrubs (or subherbaceous perennials when young) of higher elevations, the branchlets thick, coarse, often gnarled, pithy and weak; leaves simple, large, usually lobate and dentate but in some species subentire, several-ranked, usually conspicuously lighter below than above, pinnately nerved, reticulate, varying considerably according to position on the plant; inflorescence a large, graceful panicle, terminal, subterminal, or lateral from the branchlets; bracts and

bractlets small and narrow, frequently caducous; pedicels slender; flowers numerous, apetalous, whitish; sepals 2, usually oblong or elliptic, concave, sessile; stamens few to many, invested by the sepals, the anthers slender, the filaments short; ovary fusiform, stipitate, bearing a single basifixed ovule; style slender; stigma bilamellate, extended beyond the sepals and stamens, very conspicuous; fruit somewhat fleshy, dehiscing by 2 lateral valves opening first from the base, the replum persistent after dehiscence and fall of the seed; the single seed conspicuously arillate basally.

New World tropics and subtropics.

The genus is unusual in the family in not being herbaceous and in having apetalous flowers and a 1-seeded fruit. It must be considered as somewhat atypical of the Papaveraceae.

As here interpreted a single species occurs in Panama.

1. Bocconia frutescens L. Sp. Pl. 505. 1753.

Numerous synonyms occur for this species, most of which are listed by Hutchinson in his treatment of the genus (Kew Bull. 278. 1920.).

Small tree or shrub, or subherbaceous when young, the branchlets glabrous, frequently glaucous towards the tip; leaves very variable in size and shape, tending to be less lobate toward the tips of the twigs; petioles from almost obsolete in young leaves to several cm. long in older ones, glabrous or minutely papillose-pubescent especially above, canaliculate above, fleshy; blade more or less obovate in outline, up to 45 cm. long or longer and as much as 30 cm. wide, rounded or cuneate basally, acute apically, from subentire or moderately lobed in young leaves to pinnatisect in old leaves, the lobes usually obscurely dentate and acute, normally minutely papillose-pubescent and markedly reticulate below, subglabrous and darker above, the lateral veins prominent; inflorescence commonly 30 cm. long or longer, essentially glabrous; bracts linear-lanceolate, the lower ones as much as 2 or 3 cm. long, the bractlets about 5 mm. long; flowers many, relatively unattractive; sepals 2, oblong-elliptic, about 1 cm. long, obtuse and abruptly short-acuminate, subglabrous; stamens 12 or more, the filaments very slender, about 3 mm. long, the anthers linear, 6–7 mm. long; ovary 3–4 mm. long, glabrous, the stipe 4–10 mm. long; style as much as 6 mm. long; stigma bilamellate, tomentulose above, the lamellae about 5 mm. long; fruit ellipsoidal, the locule in maturity about 1 cm. long, dehiscent as described for the genus.

Mexico, Central America and West Indies to middle South America.

CHIRIQUÍ: Bajo Chorro, *Davidson 84;* Boquete, *Pittier 2879;* Cerro Punta, *Allen 309;* Río Chiriquí Viejo, *Allen 1593;* Volcán de Chiriquí, *Davidson 920; Woodson, Allen & Seibert 867.* COCLÉ: El Valle de Antón, *Hunter & Allen 314.* DARIÉN: Cana, *Williams 805.*

A number of the cited specimens might well key to such species as *B. arborea, B. Pearcei* or *B. integrifolia* in Hutchinson's treatment of the genus. However, in comparing Panamanian material with that of Mexico, other parts of Central America, the West Indies and South America it becomes clear that Hutchinson's

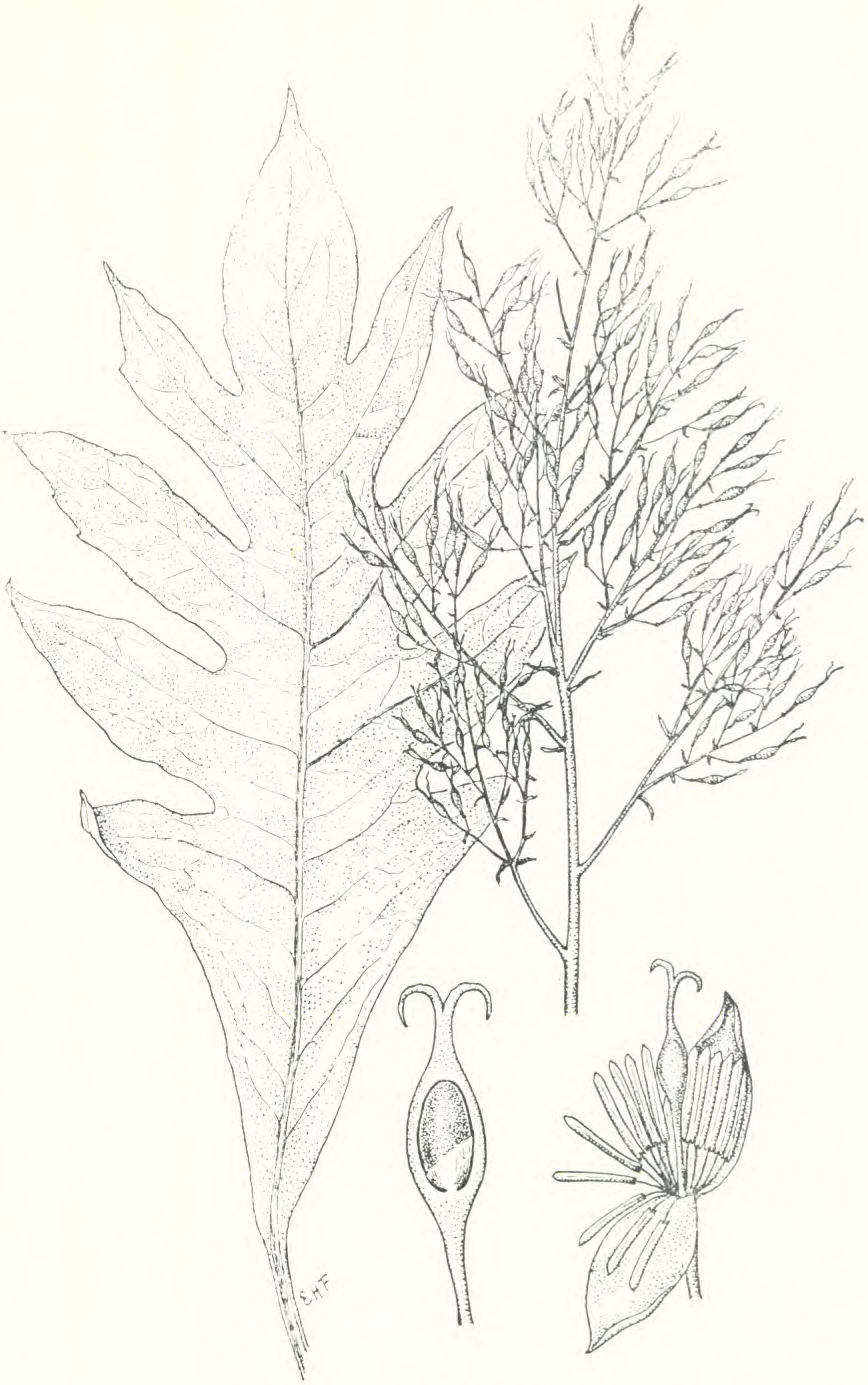

Fig. 44. *Bocconia frutescens*

specific distinctions break down in Panama, where intermediacy and probable hybridization are found. In particular the Darién specimen (*Williams 805*) much resembles the Colombian *B. integrifolia* (ex char.), but its only large leaf has a few lobations and the petiole has less pubescence than described for that species. One would judge here an intermediate condition between *B. frutescens* and *B. integrifolia.* The *Davidson 84* collection also appears quite distinctive, possessing smaller glabrous leaves and very condensed internodes not typical of the species. Yet this may be but a reflection of a disadvantageous or seasonal environment at the unusually high altitude where collected. Still other specimens might be considered equally well either *B. arborea* (Mexican type) or *B. frutescens.* It is felt that all these specimens had better be regarded as one species (incidentally all had been originally determined in herbaria as a single species, *B. frutescens*), at least until further collections may permit more comprehensive analysis.

2. ARGEMONE L.

Argemone L. Sp. Pl. 508. 1753.

Echtrus Lour. Fl. Cochinch. 1:344. 1790.

Herbs or rarely shrubs, usually glaucous and armed with prickles, the juice or sap yellowish; leaves alternate, sessile, pinnatifid to repand-lobate, the lobes spinulose-dentate and rigidly spined terminally; flowers large, solitary, terminal, or terminal on short axillary branches and thus appearing somewhat racemose or cymose, usually yellow or cream, rarely in some species red or purple; buds erect; sepals 2 or 3, usually bearing prickles, early caducous; petals 4–6, large and showy; stamens many; ovary ovoid to obovoid, many-ovulate, with 3–6 parietal placentae, usually armed; style short; stigma depressed, the lobes radiating from the center; capsule usually oblong, spiny, opening by 3–6 valves at the top; seeds crested, scrobiculate.

Temperate, subtropical, and to a lesser extent tropical regions of the New World; naturalized in Old World.

A "typical" genus of the family. A single species occurs in Panama.

1. Argemone mexicana L. Sp. Pl. 508. 1753.

Echtrus trivialis Lour. Fl. Cochinch. 1:344. 1790.
Argemone ochroleuca Sweet, Brit. Fl. Gard. 3: *pl. 242.* 1828; fide Standl. & Steyerm.
Argemone mexicana var. *ochroleuca* (Sweet) Lindl. in Bot. Reg. *pl. 1343.* 1830.

Coarse, prickly annual of sunny habitats, seldom as much as 1 m. tall; stems fleshy, lightly setose-spinose, containing a yellow sap; leaves moderate, sessile, the blade mostly obovate in outline, 5–25 cm. long and up to 8 or 9 cm. wide, the upper leaves smaller, irregularly lobed or incised, the lobes spinose-dentate and rigidly mucronate at the apex, glabrous, glaucous, pinnate-veined, the lateral veins few, obscurely and laxly reticulate; inflorescence as described for the genus; sub-

tending bracts consisting of 2–3 very reduced leaves from condensed nodes; flowers showy, light or dark yellow; sepals 3, roughly ovate, about 2 cm. long, rigidly mucronate-spinose apically, usually bearing a few smaller spines below, glabrous and glaucous; petals normally 6, broadly obovate, mostly 2–4 cm. long, glabrous, more or less parallel-veined. Capsule usually oblongoid, 4- to 6-valvate, prominently spinose; seeds many, from 4–6 parietal placentae, globose, reticulate, glabrous.

Southern United States and Mexico to Argentina and Chile; West Indies. Naturalized into Old World.

COLÓN: Santa Rita trail, *Cowell 114*.

Nine additional specific synonyms are listed by 'Kew Index' for this species; also quite a number of untenable or doubtfully tenable varieties and subvarieties have been proposed by Fedde and others. Probably critical study of the genus would indicate still other synonyms for this early name.

The TOVARIACEAE probably are represented in Panama by *Tovaria pendula* R. & P., although it has not yet been collected there. The species is known to extend from southern Mexico to Peru.

The MORINGACEAE are represented in Panama by *Moringa oleifera* Lam., the "Horseradish Tree" or *marango*. A native of Africa and the Netherlands East Indies, the species is commonly planted for hedges and ornamental trees. The seeds are utilized in the production of ben oil, of commercial value as a lubricant of watches and other delicate mechanisms. The English vernacular name arises from the flavor and odor of the roots.

CAPPARIDACEAE

Trees, shrubs, or herbs, frequently with glandular, lepidote, or stellate indument, occasionally spiny; leaves alternate, rarely opposite, simple or palmately compound, frequently 1-foliolate, stipulate or exstipulate, usually entire, rarely minutely serrate; inflorescence indeterminate, simple or compound, occasionally reduced to a single flower, bracteate or ebracteate; flowers hermaphrodite or monoecious through abortion, regular or obliquely irregular; sepals usually 4, valvate, imbricate, or open in the bud, occasionally concrescent and rupturing irregularly at anthesis; petals 4, rarely 0, equal or unequal, usually unguiculate, imbricate, valvate, or open in the bud; receptacle usually elongated into a prominent gynophore or androgynophore, frequently with glandular or eglandular disk elaborations; stamens few to many, equal or unequal, more or less declinate as a rule; filaments usually connate at the very base and free or attached to an androgynophore, inflexed or contorted in the bud; anthers 4-celled, dehiscing longitudinally, dorsifixed near the base; ovary usually borne upon a more or less elongate gynophore, occasionally sessile or subsessile, 2-carpellate, 1-celled with 2 parietal

placentas, rarely 2- to 4-celled by false septation; stigma capitate or shortly 2-lobed, sessile or stipitate; ovules campylotropous, usually numerous; fruit a dry silique dehiscing by 2 valves from a prominent replum, or fleshy and indehiscent or tardily dehiscent and without a definite replum; seeds usually cochleate-reniform, with or without an aril, without endosperm, the embryo arcuate or coiled.

A family predominantly of the tropics of both hemispheres. Beside the genera enumerated below, the genus *Morisonia* may be expected in Panama; it is closely related to *Steriphoma* in the concrescent calyx, but the stamens are included within the flowers, which lack the brilliant orange indument of *Steriphoma*. Although numerous Capparidaceae are woody, none reach sufficient size to produce usable timber. The family is chiefly noted for its production of "capers" *(alcaparras)*, which are the pickled flower buds and young fruits of *Capparis spinosa*, and for a few species of *Cleome*, particularly *C. spinosa*, which are cultivated as ornamentals in temperate climates.

a. Herbs, sometimes suffrutescent; fruit a dry, thin-walled silique, dehiscing from a distinct, double replum.
  b. Flowers hermaphrodite; replum straight and persistently joined at the apex after dehiscence of the silique; seeds without an aril .... 1. CLEOME
  bb. Flowers monoecious; replum separating at the apex and contorted after dehiscence of the silique; seeds arillate .... 2. PODANDROGYNE
aa. Shrubs and trees; fruit fleshy and tardily dehiscent or indehiscent, without a distinct replum.
  b. Flowers with 4 distinct sepals.
    c. Leaves compound, 3-foliolate; flowers hermaphrodite or unisexual by abortion; disc thick and conspicuous .... 3. CRATAEVA
    cc. Leaves apparently simple, 1-foliolate; flowers hermaphrodite; disc thin and inconspicuous .... 4. CAPPARIS
  bb. Sepals concrescent, rupturing irregularly at anthesis .... 5. STERIPHOMA

1. CLEOME L.

CLEOME L. Sp. Pl. 671. 1753.

Pedicellaria Schrank in Roem. & Usteri, Mag. f. Bot. 3:10. 1788.
Gynandropsis DC. Prodr. 1:237. 1824, in major part.
Podogyne Hoffmsgg. Verz. Pfl. Nachtr. 185. 1840. (For other generic synonyms cf. Dalla Torre & Harms, Gen. Siph. 192. 1901.)

Herbs, sometimes suffrutescent, rarely clambering, frequently glandular-pubescent or thorny; leaves alternate, stipulate or exstipulate, usually palmately compound, occasionally simple, the leaflets entire or minutely callose-serrulate; inflorescence racemose, terminal or both terminal and lateral, few- to many-flowered, bracteate, rarely ebracteate; calyx deeply 4-parted, persistent or deciduous; petals 4, more or less unequal, usually unguiculate; disc usually present, symmetrical or asymmetrical, rarely absent; stamens 6, rarely 4, inserted on a short or more or less elongate androgynophore, occasionally nearly sessile, the filaments more or less unequal and declinate; ovary borne upon a more or less elongate gynophore, rarely nearly sessile, the stigma sessile or stipitate, the ovules numerous; fruit a dry, terete silique, dehiscing from the persistently joined replum by 2 valves; seeds cochleate-reniform, smooth, minutely tuberculate, or transversely rugose.

Fig. 45. *Cleome longipes*

a. Large clambering thorny subshrubs; fruiting gynophores several times longer than the pedicels; seeds irregularly subquadroid; flowers with a conspicuous disc persisting in the fruit.......... 1. C. LONGIPES
aa. Erect or ascending annual herbs; fruiting gynophores shorter than the pedicels to somewhat longer; seeds cochleate-reniform.
b. Plants armed with stout spines at the nodes and occasionally upon the petioles.
c. Plants relatively stout, conspicuously glandular-pubescent; leaflets 5–7; flowers relatively large, pink, occasionally white; fruiting gynophores about as long as the pedicels.......... 2. C. SPINOSA
cc. Plants relatively slender, inconspicuously pubescent; leaflets 3–5, the lowermost frequently 1; flowers relatively small, green to greenish-purple; fruiting gynophores much shorter than the pedicels.......... 3. C. PANAMENSIS
bb. Plants unarmed.
c. Flowers with a conspicuous glandular disc persisting in fruit.
d. Fruiting gynophores longer than the pedicels.......... 4. C. PUBESCENS
dd. Fruiting gynophores shorter than the pedicels.......... 5. C. PILOSA
cc. Flowers without a glandular disc, or the disc not well manifest and not obvious in fruit.
d. Inflorescence with foliaceous bracts; fruiting gynophores well manifest.
e. Plants relatively stout; leaflets 5–9; flowers large and showy with a conspicuous androgynophore; seeds smooth or irregularly tuberculate.......... 6. C. SPECIOSA
ee. Plants relatively slender; leaflets 3; flowers rather small, without a conspicuous androgynophore; seeds very strongly transverse-rugose.......... 7. C. CILIATA
dd. Inflorescence without bracts, or the bracts extremely reduced; fruiting gynophores nearly obsolete.......... 8. C. SERRATA

1. CLEOME LONGIPES Lamb. ex DC. Prodr. 1:239. 1824.

Cleome scandens Ruiz ex Eichl. in Mart. Fl. Bras. 13^1:251. 1865, nom. nud. in synon.

Giant suffrutescent herbs; stems as much as 8 m. tall and 2–3 cm. in diameter at the base, trailing or clambering over neighboring plants, inconspicuously pilosulose to glabrate, armed with yellow thorns which are paired and particularly prominent at the nodes; leaves alternate, petiolate, palmately compound, the petioles 2–8 cm. long, armed with stout yellow thorns, the leaflets 3–5, ovate-elliptic, acute, cuneate, 2.5–8.0 cm. long, 1–3 cm. broad, essentially glabrous, but the midrib beneath frequently armed with thorns similar to those of the petiole; inflorescence a dense, terminal, many-flowered raceme 5–15 cm. long, the peduncle minutely pilosulose and frequently armed with small thorns, greatly accrescent in fruit, the bracts minute and setose, or suppressed, the pedicels about 1 cm. long; sepals 4, ovate-lanceolate, narrowly acuminate, about 3–4 mm. long, papillate; petals broadly elliptic, 6–8 mm. long, greenish, unguiculate, the narrow claw about ⅓ as long as the blade; stamens 6, the filaments about 5 mm. long, inserted near the base of the androgynophore, the anthers about 3 mm. long; disc conspicuous, glandular, concentric, about 1.5 mm. in diameter; ovary about 1.5 mm. long, glabrous, the stigma sessile, the gynophore about 1 mm. long, very greatly accrescent in fruit; silique linear-fusiform, 8–20 cm. long, about 1.5 mm. thick, irregularly moniliform, glabrous, seeds roughly subquadroid, about 1 mm. square, brownish-granulose, the fruiting gynophores 25–30 cm. long, pendulous.

Costa Rica to Peru.

BOCAS DEL TORO: Changuinola valley, *Dunlap 584, 333;* Nievecita, *Woodson & Schery 1025.* DARIÉN: Tucuti, Chepigana Distr., *Terry & Terry 1399;* Marraganti, *Williams 639.*

2. CLEOME SPINOSA Jacq. Enum. Pl. Carib. 26. 1760.

Cleome heptaphylla L. Sp. Pl. ed. 2. 937. 1763.
Cleome pungens Willd. Hort. Berol. *t. 18.* 1803.
Cleome horrida Mart. ex Roem. & Schult. Syst. 7:32. 1829.
Cleome spinosa var. *horrida* (Mart.) Fawc. & Rendle, Fl. Jam. 3:226. 1914.

Relatively stout herbs as much as 1.5 m. tall; stems conspicuously glandular-pubescent, armed with prominent paired thorns at the nodes; leaves alternate, petiolate, palmately compound, the petioles 2–8 cm. long, glandular-pubescent and usually armed with rather stout, yellow thorns, the leaflets 5–7, elliptic-oblanceolate, acute, narrowly cuneate, 2–10 cm. long, conspicuously pubescent and the midribs occasionally aculeolate beneath; inflorescence a many-flowered, corymbose raceme, the peduncle densely glandular-pubescent, greatly elongating in fruit, the bracts foliaceous, sessile and more or less cordate, 0.1–3.0 cm. long, the pedicels about 2 cm. long, glandular-puberulent; sepals 4, oblong-elliptic, acuminate, about 5–8 mm. long, densely glandular-puberulent; petals obovate-spatulate, 1–2 cm. long, unguiculate, the claw about ¼ as long as the blade, bright pink, occasionally white; stamens 6, the filaments attached somewhat above the base of the androgynophore, somewhat longer than the petals, the anthers about 8 mm. long; disc very inconspicuous, not obvious in fruit; ovary about 3 mm. long, glabrous, the stigma sessile, the gynophore about 2 cm. long, somewhat accrescent in fruit; silique narrowly fusiform, 5–12 cm. long, about 2–4 mm. thick, continuous or slightly moniliform, glabrous or somewhat glandular-puberulent; seeds cochleate-reniform, about 2 mm. long, light buff, smooth or minutely tuberculate; fruiting gynophores 2–3 cm. long, about equaling the pedicels or slightly longer, somewhat deflexed.

Widely distributed in tropical America and frequently cultivated as an ornamental annual in temperate latitudes.

COLÓN: vicinity of Colón, *Cowell 95.*

It is hard to tell whether the specimen cited is indigenous or an escape from cultivation.

3. CLEOME PANAMENSIS Standl. in Jour. Wash. Acad. Sci. 17:252. 1927.

Cleome Houstoni of several authors, not R. Br.

Rather weak annual herbs as much as 6 dm. tall; stems inconspicuously pubescent to essentially glabrous, usually armed with rather inconspicuous, paired thorns at the nodes; leaves alternate, the upper palmately compound, the lowermost frequently simple, the petioles 2–7 cm. long, sparsely pilosulose to essentially glabrous, usually bearing rather sparse, inconspicuous spines, the leaflets 3–5, rather broadly elliptic, narrowly acuminate, cuneate, 2–7 cm. long, essentially glabrous, the midrib infrequently with minute spines beneath; inflorescence a few- to several-flowered raceme, the peduncle minutely puberulent, elongate in fruit, the bracts foliaceous, 0.2–1.5 cm. long, distinctly stipitate, the pedicels 1.0–1.5 cm. long, very slender, minutely puberulent-papillate; sepals 2–3 mm. long, lanceolate,

minutely glandular-puberulent; petals green to greenish-purple, 3–6 mm. long, unguiculate, the claw about ⅓ as long as the blade; stamens 6, the filaments attached at the base of the androgynophore, about 2 mm. long, the anthers about 3–4 mm. long; disc clearly manifest, persisting in fruit; ovary about 3 mm. long, glabrous or minutely papillate, the stigma borne upon a rather slender style persisting in fruit, the gynophore about 1 mm. long, accrescent in fruit; silique narrowly fusiform, 3–6 cm. long, about 2 mm. thick, rather obscurely moniliform, glabrous; seeds cochleate-reniform, yellow-buff, about 1.5 mm. long, smooth or very minutely granulose; fruiting gynophores much shorter than the pedicels, about 5 mm. long.

Known with certainty only from Panama, but possibly extending into Colombia.

CANAL ZONE: Frijoles, *Pittier 3751*; Margarita Swamp, south of France Field, *Maxon & Valentine 7066;* Miller Pt., Barro Colorado Island, *Aviles 993;* end of Pearson Trail, Barro Colorado Island, *Bangham 576*. DARIÉN: Marraganti, *Williams 993*.

The interpretation of this species has been somewhat difficult. In describing it, Standley allied it to *C. aculeata*, which he noted to differ in having coarsely tuberculate seeds. *C. aculeata* also differs in having a sessile stigma and in the absence of a manifest disc. My interpretation of *C. panamensis* includes specimens previously included under *C. Houstoni* by Standley (Fl. Panama Canal Zone, 185. 1928). This species of the Antilles differs from *C. panamensis* in its stouter, more viscid-glandular habit, its longer fruiting gynophores, its more strongly developed disc, and its larger, bright pink flowers.

4. CLEOME PUBESCENS Sims in Curt. Bot. Mag. *t. 1857*. 1816.

Rather stout herbs as much as 1.5 m. tall; stems densely glandular-pubescent to essentially glabrous, unarmed; leaves alternate, palmately compound, the petioles 7–15 cm. long, pilose, the leaflets 5–7, elliptic to oblanceolate-elliptic, acuminate, narrowly cuneate, 5–14 cm. long, essentially glabrous or minutely glandular-puberulent beneath; inflorescence a many-flowered raceme, the peduncle densely glandular-puberulent, greatly elongate in fruit, the bracts foliaceous, distinctly petiolate, the uppermost about 2 mm. long, grading downward to the foliage leaves, the pedicels about 1.5 cm. long, densely glandular-puberulent, accrescent in fruit; sepals about 3 mm. long, ovate, acuminate, sparsely glandular-puberulent; petals pink or white, obovate, about 1.5 cm. long, sessile; stamens 6, the filaments very unequal, attached somewhat above the base of the androgynophore, 1.5–2.0 cm. long, the anthers about 5 mm. long; disc very distinct and glandular, eccentric, persisting in fruit; ovary about 5 mm. long, minutely puberulent-papillate, the stigma nearly sessile, the gynophore about 1 cm. long, greatly accrescent in fruit; silique narrowly fusiform, 5–10 cm. long, about 3–5 mm. thick, continuous, minutely and rather sparsely puberulent; seeds cochleate-reniform, about 1.5 mm. long, brown, minutely and rather sparsely tuberculate; fruiting gynophores longer than the pedicels, 4–5 cm. long, essentially straight.

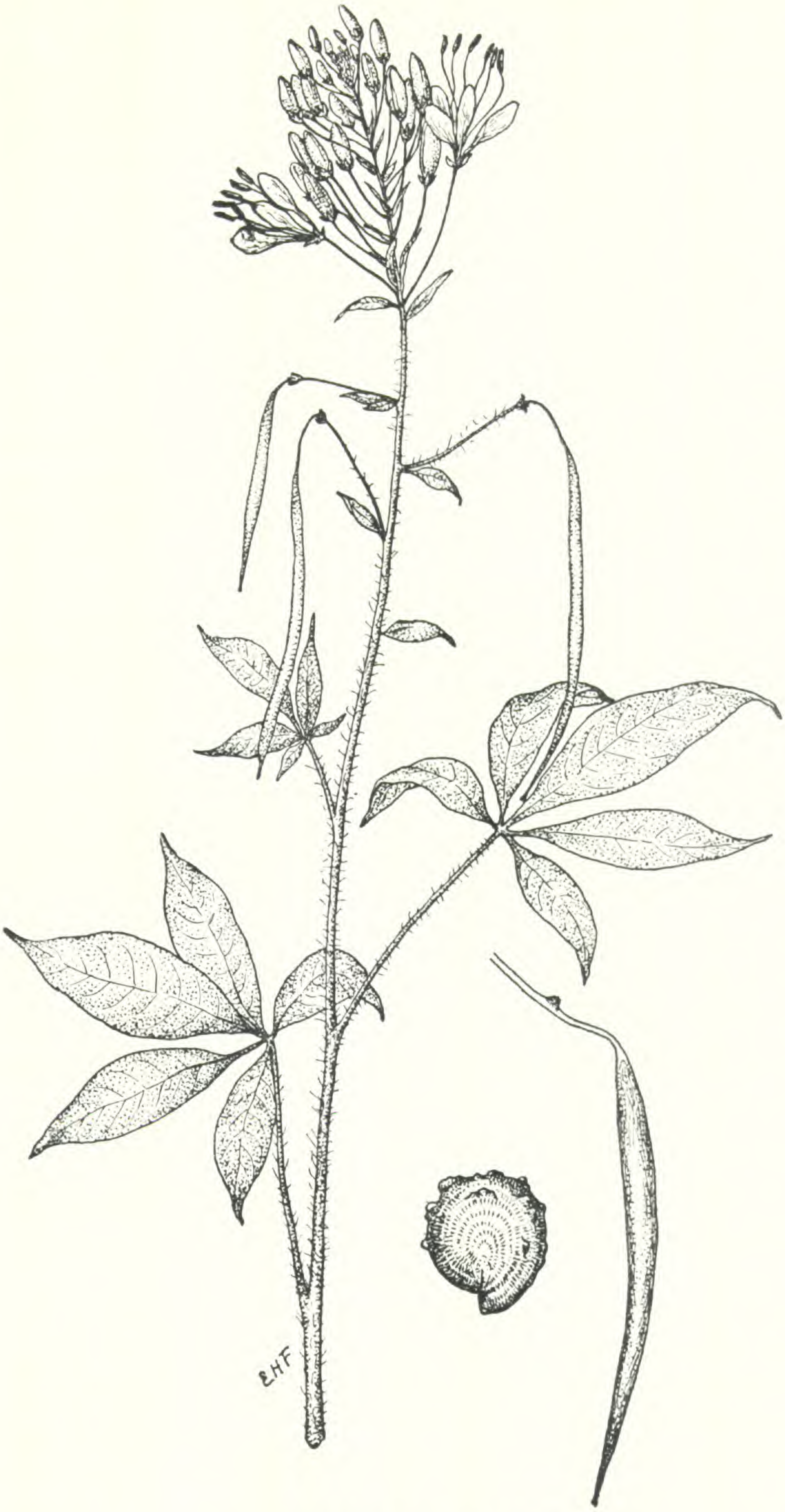

Fig. 46. *Cleome pilosa*

Costa Rica to Brazil; Dominican Republic.

DARIÉN: Boca de Pauarandó, Sambú River, alt. 20 m., *Pittier 5586*. VERAGUAS: Isla de Uva, Contreras group, *Pittier 5514*.

5. CLEOME PILOSA Benth. Bot. Voy. Sulphur 65. 1844.

Cleome pilosa var. *costaricensis* Donn. Sm. in Bot. Gaz. 23:235. 1897.
Cleome Pittieri Briq. in Ann. Cons. & Jard. Bot. Genève 17:370. 1914.

Rather stout herbs as much as 1.5 m. tall; stems glandular-pubescent, unarmed; leaves alternate, palmately compound, the petioles 5–25 cm. long, pilose, the leaflets 5–10, or the uppermost 3, oblanceolate-elliptic, subcaudate-acuminate, narrowly cuneate, 3–25 cm. long, 1–5 cm. broad, either surface with sparse, strigose hairs; inflorescence a many-flowered raceme, the peduncle densely glandular-puberulent, greatly elongate in fruit, the bracts foliaceous, petiolate, grading to the uppermost foliage leaves, the pedicels 1.5–2.0 cm. long, densely glandular-puberulent, accrescent in fruit; sepals ovate, acuminate, 2–3 mm. long, glandular-papillate; petals pink or pinkish-lavender, obovate, 1.0–1.5 cm. long, sessile; stamens 6, the filaments 1.0–1.5 cm. long, attached somewhat above the base of the androgynophore, the anthers about 5 mm. long; disc very prominent and eccentric, persisting in fruit; ovary about 5 mm. long, papillate, the gynophore 0.5–1.0 cm. long, accrescent in fruit; silique narrowly fusiform, 6–10 cm. long, glabrous; seeds cochleate-reniform, about 1.5 mm. long, yellowish buff, smooth or inconspicuously tuberculate; fruiting gynophores shorter than the pedicels, 1–2 cm. long.

Southern Mexico to Colombia and Venezuela.

BOCAS DEL TORO: Lincoln Creek, Changuinola valley, *Dunlap 573*. CANAL ZONE: along Chagres River, between Gamboa and El Vigía, *Pittier 2366;* between Gorgona and Mamei, alt. 10–30 m., *Pittier 2250;* vicinity of Madden Dam, alt. 50–75 m., *Seibert 558;* Río Paraíso, above East Paraíso, *Standley 29855;* Madden Dam, *Porterfield s. n.;* near Alhajuela, *Killip 3216;* forests on dry limestone, around Alhajuela, alt. 30–100 m., *Pittier 2366*.

C. pilosa and *C. pubescens* are distinguishable almost solely by the relative lengths of the fruiting pedicels and gynophores, and it may well be doubted that they are sufficiently separated as species.

6. CLEOME SPECIOSA HBK. Nov. Gen. & Sp. 5:84. *t. 436*. 1821.

Gynandropsis speciosa (HBK.) DC. Prodr. 1:238. 1824.

Stout herbs 1 m. or more tall; stems sparsely pilosulose to essentially glabrous, unarmed; leaves alternate, palmately compound, the petioles 2–12 cm. long, irregularly pilosulose to essentially glabrous, the leaflets 5–9, or the uppermost 3, oblanceolate, acuminate, very narrowly cuneate-decurrent, 5–25 cm. long, 1–4 cm. wide, sparsely pilosulose to glabrous; inflorescence a several- to many-flowered, corymbiform raceme, the peduncle somewhat accrescent in fruit, the bracts foliaceous, sessile, cordate, grading to the uppermost leaves, the pedicels 3–4 cm. long, sparsely pilosulose to glabrous, somewhat accrescent in fruit; sepals ovate, long-acuminate, 4–5 mm. long, sparsely pilosulose; petals oblanceolate-spatulate,

2.5–3.5 cm. long, bright pink or rose-purple, unguiculate, the claw about ¼ as long as the blade; stamens 6, the filaments 3–5 cm. long, attached about 5–7 mm. above the base of the androgynophore, the anthers 7–8 mm. long; disc absent or obsolete; ovary about 1 cm. long, minutely papillate, the stigma nearly sessile, the gynophore 2.0–2.5 cm. long, accrescent in fruit; silique 6–10 cm. long, about 2 mm. thick, continuous or obscurely moniliform, glabrous; seeds cochleate-reniform, dark brown, about 2.5 mm. long, prominently but irregularly tuberculate; fruiting gynophores much longer than the pedicels, 3–5 cm. long.

Southern Mexico to northern South America.

CANAL ZONE: vicinity of Gatuncillo, *Piper 5644;* Paraíso, *Hayes 107.* PANAMÁ: Capira, *Paul 129.*

The genus *Gynandropsis* is not recognized in this treatment since it is quite impossible for us to distinguish it from *Cleome* in the phraseology adopted by certain recent floras. In no species of *Cleome* known to us can the staminal filaments truthfully be described as "free from the gynophore." In some species, the attachment of the stamens is quite at the base of the gynophore, but in others, as in *C. spinosa, C. pubescens,* and *C. pilosa,* as well as in many others outside Panama, an androgynophore only slightly shorter than that of *C. speciosa* is present, and may be seen quite clearly in fruiting specimens.

7. CLEOME CILIATA Schum. & Thonn. in Dansk. Vidensk. Selsk. Skr. Nat. & Mat. Afh. 4:68. 1829.

Cleome guineensis Hook. f. in Hook. Niger Fl. 218. 1849.

Rather slender herbs less than 1 m. tall; stems sparsely and inconspicuously pilosulose to glabrous, unarmed; leaves alternate, palmately compound, the petioles 2–4 cm. long, sparsely pilosulose to glabrate, the leaflets 3, rhombic-elliptic, acute, cuneate, 1.5–4.0 cm. long, sparsely pilosulose to essentially glabrous; inflorescence a few-flowered raceme, the bracts 3-foliolate and grading to the uppermost leaves, or the uppermost entire, the pedicels about 2 cm. long, essentially glabrous, slightly accrescent in fruit; sepals narrowly lanceolate, acuminate, about 4 mm. long, sparingly glandular-puberulent; petals oblanceolate-spatulate, pink, about 8 mm. long, unguiculate, the claw about ¼ as long as the blade; stamens 6, the filaments very unequal, 4–6 mm. long, the lower half somewhat thickened, attached to the base of the gynophore, the anthers about 2 mm. long; ovary 4–5 mm. long, rather sparsely glandular-papillate, the stigma distinctly stipitate, the gynophore about 2 mm. long, accrescent in fruit; silique about 4 cm. long, about 3 mm. thick, continuous, glabrous; seeds cochleate-reniform, orange-buff, very strongly transverse-rugose, about 1.5 mm. long; fruiting gynophore much shorter than the pedicels, about 5 mm. long.

Western tropical Africa; introduced into Jamaica, Trinidad, and Panama.

CANAL ZONE: Matachin to Las Cascadas, *Cowell 332.*

The first record of this species for continental America.

8. CLEOME SERRATA Jacq. Enum. Pl. Carib. 26. 1760.

Cleome polygama L. Sp. Pl. ed. 2. 939. 1763.

Rather slender herbs seldom attaining 1 m. in height; stems essentially glabrous, unarmed; leaves palmately compound or the lower simple, the petioles 3–6 cm. long, scatteringly pilosulose to glabrous, the leaflets 3–1, lanceolate to ovate, acuminate, obtuse at the base, 3–15 cm. long, 1–6 cm. broad, minutely callose-serrulate, essentially glabrous; inflorescence a rather few-flowered raceme, the peduncle essentially glabrous, somewhat elongated in fruit, the bracts setose and caducous or obsolete, the pedicels 1.0–1.5 cm. long, essentially glabrous, somewhat accrescent in fruit; sepals ovate-lanceolate, acuminate, 4–5 mm. long, glabrous; petals elliptic-oblanceolate, about 8 mm. long, pale purple or greenish to white; stamens 6, the filaments 5–7 mm. long, attached somewhat above the base of the androgynophore, the anthers about 4 mm. long; disc obsolete; ovary about 5–6 mm. long, glabrous, the stigma sessile, the gynophore about 2 mm. long, not elongating in fruit; silique about 4–8 cm. long, about 3 mm. thick, glabrous; seeds cochleate-reniform, dark brown, conspicuously tuberculate, about 2 mm. long.

Southern Mexico to Colombia; Cuba and Jamaica.

CANAL ZONE: near Corozal, *Gervais 146*. COLÓN: between France Field and Catival, *Standley 30433*; around Porto Bello, alt. 5–100 m., *Pittier 2472*. DARIÉN: Marraganti, *Williams 656*; Yape, alt. 30 m., *Allen 852*. PANAMÁ: between Las Sabanas and Matías Hernández, *Standley 31924*.

2. PODANDROGYNE Ducke

PODANDROGYNE Ducke in Archivos Jard. Bot. Rio Jan. 5:115. 1930.

Gynandropsis DC. Prodr. 1:237. 1824, in part.

Erect or ascending, suffrutescent or suffruticose herbs; leaves alternate, simple or palmately compound, exstipulate; inflorescence racemose or corymbose, terminal, several- to many-flowered, bracteate or ebracteate; flowers monoecious, or occasionally dioecious through abortion, the lower flowers pistillate, the upper staminate; calyx more or less deeply 4-parted, persistent or deciduous, sometimes more or less petaloid; petals 4, more or less unequal, usually unguiculate; disc usually manifest, symmetrical or eccentric; fertile stamens 6, inserted on a short or moderately elongate androgynophore, the filaments somewhat unequal and declinate, the anthers dorsifixed near the base, accompanied by an abortive, nearly sessile pistillode; fertile ovary borne upon a manifest gynophore of moderate length, the stigma capitate, shortly stipitate, the ovules numerous, the accompanying staminodia borne upon a manifest androgynophore, greatly reduced, sagittate; fruit a dry, terete silique, dehiscing irregularly, the replum finally separating at the tip and irregularly contorted; seeds cochleate-reniform, smooth or granulate, with a conspicuous, lamellate, funicular aril.

1. Podandrogyne chiriquensis (Standl.) Woodson, comb. nov.

Gynandropsis chiriquensis Standl. in Jour. Wash. Acad. Sci. 17:252. 1927.
Gynandropsis pulcherrima Standl. loc. cit. 253. 1927.

Suffruticose herbs 1–3 m. tall, the stem simple or branching, more or less conspicuously ferruginous-pilosulose to essentially glabrous; leaves alternate, long-petiolate, palmately compound or the uppermost rarely simple, the petioles 2–20 cm. long, inconspicuously pilosulose to essentially glabrous, the leaflets 3–7, shortly petiolulate, elliptic to obovate, acuminate, cuneate, the median largest, 4–20 cm.

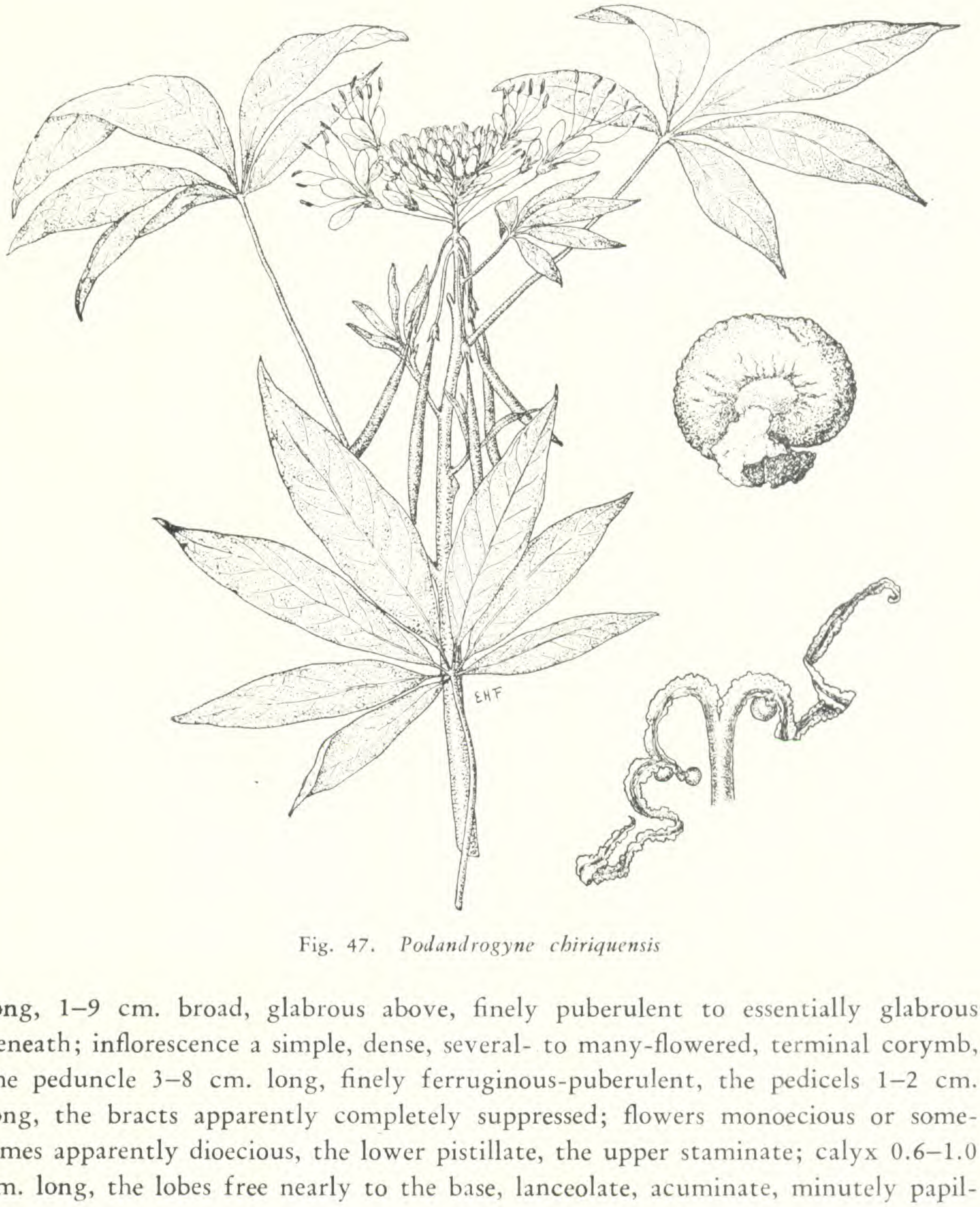

Fig. 47. *Podandrogyne chiriquensis*

long, 1–9 cm. broad, glabrous above, finely puberulent to essentially glabrous beneath; inflorescence a simple, dense, several- to many-flowered, terminal corymb, the peduncle 3–8 cm. long, finely ferruginous-puberulent, the pedicels 1–2 cm. long, the bracts apparently completely suppressed; flowers monoecious or sometimes apparently dioecious, the lower pistillate, the upper staminate; calyx 0.6–1.0 cm. long, the lobes free nearly to the base, lanceolate, acuminate, minutely papil-

late, green or somewhat petalaceous; petals ovate-spatulate, unguiculate, 0.8–1.8 cm. long, brilliant red or reddish-orange, the claw about ⅓ as long as the blade; fertile stamens widely exserted, the filaments 2–3 cm. long, glabrous, the anthers about 0.5 cm. long, the androgynophore 1–3 mm. long; fertile pistil oblong-fusiform, 1.0–1.5 cm. long, densely papillate, the capitate stigma borne upon a short style, the gynophore 2–3 mm. long, elongating after pollination, the staminodia about 2 mm. long; siliques pendulous, linear-fusiform, 4–13 cm. long, about 4 mm. broad, continuous, glabrous, the fruiting gynophore 1.0–2.5 cm. long, the seeds pale ashy brown, indistinctly granulate, about 3 mm. long.

Costa Rica to Panama.

BOCAS DEL TORO: Buena Vista, *Cooper 220*. CHIRIQUÍ: valley of the upper Río Chiriquí Viejo, alt. 1300–1900 m., *Seibert 138*, *G. White 168*; vicinity of Cerro Punta, alt. 2000 m., *Allen 1560*, *White & White 50*; Bajo Chorro, Boquete Distr., alt. 6000 ft., *Davidson 180*; vicinity of Bajo Mona and Quebrada Chiquero, alt. 1500 m., *Woodson & Schery 539*; along Río Caldera below Quiel, *Pittier 3145*; Casita Alta, Volcán de Chiriquí, alt. 1500–2000 m., *Woodson, Allen & Seibert 859*; valley of upper Río Gariché, alt. 1050–1100 m., *Seibert 334*. COCLÉ: La Mesa, along trails in cleared areas, *Allen 2730*; vicinity of El Valle, north rim, alt. 800–1000 m., *Allen 219*; mountains beyond La Pintada, alt. 400–600 m., *Hunter & Allen 552*.

The several specimens enumerated above, as well as several not cited, may be separated in general into two groups with leaflets three or five, coinciding with Standley's primary distinction of *Gynandropsis pulcherrima* and *G. chiriquensis*, respectively. In intervening specimens, however, the leaflets may be from three to five upon the same stem, or as many as seven.

3. CRATAEVA L.

CRATAEVA L. Sp. Pl. 444. 1753.

Tapia Adans. Fam. 2:407. 1763. (For other generic synonyms cf. Dalla Torre & Harms, Gen. Siph. 192. 1901.)

Shrubs or small trees, usually glabrous; leaves alternate, palmately 3-foliolate, exstipulate; inflorescence terminal, several-flowered, corymbosely racemose; flowers hermaphrodite or unisexual through abortion; calyx deeply 4-parted, imbricate, deciduous; petals 4, open in the bud, long-ungulate; disc radially symmetrical, thick and conspicuous, adnate to the calyx tube; stamens 8–50, the filaments inserted on a short androphore; ovary borne upon an elongate gynophore, ovoid or spherical, the stigma sessile, the ovules numerous, borne upon 2 parietal placentas; fruit an indehiscent, ovoid or spherical berry borne upon an elongate, thickened gynophore.

1. CRATAEVA TAPIA L. Sp. Pl. 444. 1753.

Cleome arborea Schrad. in Goett. Gel. Anz. 707. 1821.
Crataeva gynandra L. loc. cit. ed. 2. 636. 1762.
Crataeva tapioides DC. Prodr. 1:243. 1824.
Crataeva acuminata DC. loc. cit. 1824.
Crataeva radiatiflora DC. loc. cit. 1824.
Crataeva Benthamii Eichl. in Mart. Fl. Bras. 13^1:265. 1865.

Fig. 48. *Crataeva Tapia*

Shrubs or trees to 10 m. or more tall, with grayish bark conspicuously lenticellate; leaves somewhat caducous, long-petiolate, 3-foliolate, the leaflets elliptic, acute to acuminate, obtuse or attenuate at the base, 5–20 cm. long, 1.5–8.0 cm. broad, membranaceous, glabrous or irregularly puberulent-papillate, the petiole 2–9 cm. long; inflorescence terminal, corymbose, several-flowered, somewhat exceeding the subtending leaves, the pedicels 4–8 cm. long; sepals ovate-trigonal and acuminate to obovate-elliptic and obtuse, 3–4 mm. long, glabrous; petals long-ungulate, 1.5–2.5 cm. long, white or greenish, the blade narrowly elliptic to broadly obovate; stamens variable in number, usually 16, the filaments somewhat unequal, 2–6 cm. long, glabrous, the anthers 3–4 mm. long; pistil spherical or

broadly ovoid, 3–5 mm. long, the gynophore 2–4 cm. long; mature fruit spherical or ovoid, 3–7 cm. long, the gynophore 5–7 cm. long.

CANAL ZONE: around Alhajuela, Chagres valley, alt. 30–100 m., *Pittier 3455*. CHIRIQUÍ: Puerto Armuelles, alt. 50 ft., *Davidson 1104*; Progreso, *Cooper & Slater 238*; along Río Dupí, near sea level, *Pittier 5218*. COCLÉ: Natá, *Seemann s. n.*

Called *estrella* in Chiriquí, according to Cooper and Slater. Known as "Garlic Pear Tree" in Jamaica, according to Fawcett and Rendle, because of the fetid odor of garlic emitted by all parts of the plants, including the wood, which is rather soft and coarse.

4. CAPPARIS L.

CAPPARIS L. Sp. Pl. 503. 1753.

Quadrella Meissn. Gen. 15. 1837. (For numerous other synonyms cf. Dalla Torre & Harms, Gen. Siph. 193. 1901.)

Shrubs or trees, glabrous, lepidote, or pubescent with stellate or simple hairs; leaves usually alternate, stipulate or exstipulate, the blade simple, sometimes subtended by a more or less definite petiolar pulvinus; inflorescence various, usually several- to many-flowered, bracteate; sepals 4, free or somewhat united at the base, valvate, imbricate, or open in the bud, equal or in 2 unequal series, usually subtending a fleshy or membranaceous disc gland; petals 4, equal or somewhat unequal, imbricate or open in the bud; stamens few to over 100, the filaments inserted on a discoid or cylindrical androphore; pistil 1-celled in the Panamanian species, with 2 parietal placentas bearing few to many campylotropous ovules, borne upon a short or elongate gynophore; fruit a fleshy silique, tardily dehiscent or indehiscent.

a. Indument lepidote, or of stellate hairs.
  b. Indument lepidote throughout; staminal filaments conspicuously thickened and pilose at the base.
    c. Ovary and fruit essentially sessile.
      d. Leaves coriaceous, 4–11 cm. long, rounded to broadly acute, densely lepidote beneath; inflorescence a corymbose panicle........ 1. C. ODORATISSIMA
      dd. Leaves firmly membranaceous, 15–25 cm. long, subcaudate-acuminate, inconspicuously lepidote beneath; inflorescence an elongate raceme........ 2. C. ANTONENSIS
    cc. Ovary and fruit borne upon an elongate gynophore.
      d. Corymbs clustered in the axils of the uppermost leaves, several-flowered; leaves heavily coriaceous, the petioles 0.5–1.5 cm. long........ 3. C. CYNOPHALLOPHORA
      dd. Corymbs terminal, solitary, few-flowered; leaves firmly membranaceous to subcoriaceous, the petioles 2.0–2.5 cm. long........ 4. C. CHIRIQUENSIS
  bb. Indument of stellate hairs upon flowers and leaves, occasionally lepidote upon the stem; staminal filaments glabrous, not greatly enlarged at the base.
    c. Leaves cuneate at the base.
      d. Leaves acuminate to subcaudate-acuminate; calyx cleft nearly to the receptacle, the lobes essentially free.
        e. Corymbs much shorter than the subtending leaves, the flowers not specially congested at the base of the peduncle; flowers very small, the petals about 3.5 mm. long, the gynophore much shorter than the stamens........ 5. C. CROTONANTHA

ee. Corymbs umbelliform, the flowers congested at the tip of a filiform peduncle nearly as long as the subtending leaves; flowers larger, the petals 8–10 mm. long, the gynophore longer than the stamens .... 6. C. FILIPES

dd. Leaves broadly rounded and minutely mucronulate; calyx campanulate, cleft about half way to the receptacle .... 12. C. OVALIFOLIA

cc. Leaves deeply cordate and amplexicaul, densely stellate-tomentose beneath; corymbs subumbelliform, the flowers congested at the tip of a filiform peduncle much exceeding the subtending leaves .... 7. C. MIRIFICA

aa. Indument none, or of simple hairs.

b. Sepals large and unequal, closely imbricate in the bud, abscissing shortly after anthesis.

c. Leaves obscurely cordate at the base, usually pilosulose with simple hairs, very shortly petiolate; fruit subovoid, 3–6 cm. long, densely tuberculate .... 8. C. VERRUCOSA

cc. Leaves broadly acute to rounded at the base, glabrous, distinctly petiolate; fruits oblong-siliquiform, compressed, 4–15 cm. long, smooth .... 9. C. FLEXUOSA

bb. Sepals small, essentially equal, open in the bud, persistent after anthesis.

c. Inflorescences of several-flowered racemes in the uppermost leaf-axils; leaves strikingly heteromorphic, the lower larger and definitely petiolate, the uppermost much smaller and sessile or subsessile, all with a rather definite pulvinus subtending the blade .... 10. C. BADUCCA

cc. Inflorescence of solitary flowers in the uppermost leaf-axils; leaves essentially homomorphic, the uppermost somewhat reduced in size, but all definitely petiolate, without a pulvinus .... 11. C. UNIFLORA

1. CAPPARIS ODORATISSIMA Jacq. Hort. Schoenbr. 1:57. *t. 110.* 1797.

Capparis intermedia HBK. Nov. Gen. & Sp. 5:98. 1821.

Shrubs or trees to 15 m. tall, densely lepidote throughout; leaves shortly petiolate, oval to obovate-elliptic, rounded or broadly obtuse at the tip, rounded to obtuse or broadly acute at the base, 4–11 cm. long, 2–6 cm. broad, coriaceous, glabrous above, densely lepidote beneath, the midrib conspicuously impressed, the petioles 0.5–1.0 cm. long; inflorescence terminal and occasionally lateral as well from the uppermost nodes, corymbosely paniculate, branching repeatedly, several- to many-flowered, somewhat shorter than the subtending leaves; pedicels 0.5–1.0 cm. long; bracts minute, caducous; sepals equal, valvate, forming a smooth spherical bud, oblong-elliptic, acute, 5–7 mm. long, coriaceous, densely lepidote without, subtending small trigonal glands about 1 mm. long; petals imbricate, ovate-elliptic, sessile, 7–8 mm. long, puberulent-papillate within, densely lepidote without, usually greenish white; stamens about 28, subequal, the filaments 7–9 mm. long, enlarged and pilosulose at the base, glabrous above, inserted upon a slender androgynophore somewhat less than 1 mm. long, the anthers about 1.5 mm. long; pistil oblongoid, about 3 mm. long, densely lepidote, the stigma sessile, the gynophore somewhat less than 2 mm. long, not elongating in fruit; fruits oblong-fusiform, occasionally somewhat contorted, about 4–10 cm. long, about 0.5 cm. thick, 1-seeded or if 2–3-seeded sharply articulated, minutely lepidote, without a well-manifest gynophore.

Southern Mexico to Venezuela and Peru; Antilles.

COCLÉ: in sand, La Venta Beach, *Muenscher 16313.* PANAMÁ: Taboga Island, alt. 0–250 m., *Pittier 3535, Woodson, Allen & Seibert 1496.*

2. Capparis **antonensis** Woodson, spec. nov.

Arbuscula ca. 3 m. alta; ramulis teretibus crassiusculis juventate minute lepidotis mox glabratis; foliis oblongis vel elliptico-oblongis apice subcaudato-acuminatis basi rotundatis 15–25 cm. longis 3.5–5.5 cm. latis membranaceis supra viridibus glabris subtus inconspicue lepidotis, petiolo ca. 0.5 cm. longo; inflorescentiis in axillis foliorum superiorum racemosis multifloris foliis subaequantibus; floribus ignotis; baccis siliquiformibus sessilibus 4-angularibus ca. 18 cm. longis ca 0.5 cm. crassis minute lepidotis.

Small trees about 3 m. tall; branches terete, rather stout, minutely lepidote but soon becoming glabrate; leaves oblong or elliptic-oblong, subcaudate-acuminate, rounded at the base, 15–25 cm. long, 3.5–5.5 cm. broad, membranaceous, glabrous above, inconspicuously lepidote beneath, the petioles about 0.5 cm. long; inflorescence axillary in the upper leaf axils, racemose, many-flowered, the peduncle about as long as the subtending leaves; flowers unknown; fruits siliquiform, sessile, 4-angled, about 18 cm. long and 0.5 cm. thick, minutely lepidote.

COCLÉ: hills north of El Valle, Jan. 13, 1942, *P. H. Allen 2948* (Herb. Missouri Bot. Gard., TYPE).

It is difficult to evaluate the affinities of this species since flowers are unknown. It is unlike any American species available to me for comparison.

3. Capparis cynophallophora L. Sp. Pl. 504. 1753; Fawc. & Rendle, in Jour. Bot. 52:143. 1914.

Capparis siliquosa L. Syst. 1071. 1759.
Capparis jamaicensis Jacq. Enum. Pl. Carib. 23. 1760.
Capparis torulosa Sw. Prodr. 81. 1788.
Capparis emarginata A. Rich. in Sagra, Fl. Cub. 10:28. *t. 9.* 1843.
Capparis isthmensis Eichl. in Mart. Fl. Bras. 13^1:269. 1865.

Shrubs or small trees to 6 m. tall, the branches densely lepidote to glabrate; leaves elliptic to obovate-oblong, occasionally narrowly lanceolate, apex obtuse to acuminate, base obtuse to rounded, 5–20 cm. long, 1.5–6.0 cm. broad, heavily coriaceous, glabrous above, densely lepidote beneath, the petioles 0.5–1.5 cm. long; inflorescence both terminal and in the axils of the upper leaves, corymbose, the terminal paniculate with few branches, the lateral racemose, much shorter than the subtending leaves, densely lepidote throughout, few- to several-flowered; pedicels about 1 cm. long; sepals valvate, forming a sharply 4-angled bud, equal, ovate, acute, 7–12 mm. long, coriaceous, densely lepidote without, puberulent within, subtending an ovate-trigonal, membranaceous, internal gland about 2 mm. long; petals ovate, broadly acute, sessile, 8–15 mm. long, white to purplish or brownish, densely lepidote without, puberulent within; stamens about 32, the filaments subequal, about 2 cm. long, somewhat thickened and pilose at the base, glabrous above, attached to a thickened androgynophore about 1 mm. tall, the anthers about 5 mm. long; pistil oblong-fusiform, about 2 mm. long, densely lepidote, the stigma sessile, the gynophore about 12 mm. long; elongating in fruit;

Fig. 49. *Capparis chiriquensis*

fruits linear-fusiform, more or less articulated, 15–40 cm. long, about 5–6 mm. thick, densely brown-lepidote, the gynophore 5–8 cm. long.

Southern peninsular Florida, Bahama Islands; Antilles; southern Mexico to Venezuela.

CANAL ZONE: Alajuela, *Heriberto 7;* Victoria Fill, near Miraflores Lake, *Allen 1760, 1748;* vicinity of Salamanca Hydrographic Station, Río Pequení, *Woodson, Allen & Seibert 1555.* DARIÉN: Patiño, on cliffs along the beach, *Pittier 6608;* vicinity of La Palma, alt. 0–50 m., *Pittier 5504.* PANAMÁ: Swamp on Río Jagua, near El Congor Hill, alt. 2 m., *Hunter & Allen 480;* near the big swamp east of the Río Tecúmen, *Standley 26587.*

4. CAPPARIS **chiriquensis** Woodson, spec. nov.

Arbor usque 10 m. alta; ramulis post exsiccationem valde angulatis juventate sparse lepidotis tandem glabratis cortice griseo; foliis alternatis longiuscule petiolatis obovato-ellipticis apice anguste acuminatis basi late acutis ca. 15 cm. longis 5.0–5.5 cm. latis firme membranaceis vel tenuiter coriaceis supra pallide viridibus glabris nervo medio impresso subtus dense lepidotis, petiolis 2.0–2.5 cm. longis; inflorescentiis terminalibus racemosis corymbosis paucifloris pedunculo foliis breviori, pedicellis in fructu 2.5–3.0 cm. longis; floribus ignotis; baccis siliquiformibus lineari-fusiformibus leviter articulatis ca. 40 cm. longis 4 mm. crassis dense brunneo-lepidotis, gynophoro ca. 5 cm. longo.

Trees as much as 10 m. tall; branches strongly angulate in desiccation, sparsely lepidote when young, eventually becoming glabrate, bark grayish; leaves alternate, rather long-petiolate, obovate-elliptic, apex narrowly acuminate, base broadly acute, about 15 cm. long and 5.0–5.5 cm. broad, firmly membranaceous to thinly coriaceous, above pale green, glabrous, the midrib impressed, beneath densely lepidote, the petiole 2.0–2.5 cm. long; inflorescence terminal, corymbosely racemose, few-flowered, the peduncle shorter than the subtending leaves, the pedicels in fruit 2.5–3.0 cm. long; flowers unknown; fruits siliquiform, linear-fusiform, slightly articulated, about 40 cm. long and 0.4 cm. thick, densely brown-lepidote, the gynophore about 5 cm. long.

CHIRIQUÍ: vicinity of Puerto Armuelles, alt. 0–75 m., July 28–31, 1940, *Woodson & Schery 846* (Herb. Missouri Bot. Gard., TYPE).

5. CAPPARIS CROTONANTHA Standl. in Field Mus. Publ. Bot. 4:210. 1929.

Slender trees about 8 m. tall, the branches terete, slender, stellate-tomentose when young, becoming glabrate; leaves oval or elliptic, abruptly and rather shortly subcaudate-acuminate, base rather broadly acute, 7–18 cm. long, 2.5–8.0 cm. broad, thinly membranaceous, glabrous above, stellate-puberulent beneath, the petiole about 1 cm. long; inflorescence paniculate, several-flowered, much shorter than the subtending leaves, the pedicels about 0.4 cm. long, brownish stellate-puberulent, the bracts minute, caducous; sepals equal, valvate, closed in the spherical bud, ovate-oblong, broadly acute, about 3 mm. long, finely brown stellate-puberulent, subtending hemispheric, rather fleshy, glabrous glands somewhat less than 0.5 mm. long; petals ovate, sessile, rounded at the tip, about 3.5 mm. long,

white, minutely puberulent with simple hairs; stamens 20, the filaments about 2.5 mm. long, glabrous, not enlarged at the base, attached to an androphore about 0.5 mm. long, the anthers about 1 mm. long; pistil shortly oblongoid, about 1 mm. long, glabrous, the gynophore about 1 mm. long; fruits globose, about 5 cm. in diameter "with hard green rind and white pulp."

Panama.

SAN BLAS: Permé, *Cooper 660.*

6. CAPPARIS FILIPES Donn. Sm. in Bot. Gaz. 23:2. 1897.

Capparis clara Schery, Ann. Missouri Bot. Gard. 29:351. 1942.

Small trees to about 5 m. tall; branches slender, terete, brownish lepidote when young, developing a gray bark when older; leaves oblong- to obovate-elliptic, subcaudate-acuminate, base acute, firmly membranaceous, 8–17 cm. long, 3.5–7.0 cm. broad, glabrous above, inconspicuously stellate-puberulent beneath, the petioles 0.3–0.5 cm. long; inflorescences in the axils of the uppermost leaves, umbelliform at the tip of a filiform naked peduncle 8–10 cm. long, bearing 8–10 small white flowers, the pedicels filiform, 1.5–2.0 cm. long, all minutely stellate-puberulent; sepals open in the bud, equal, trigonal, acute, 1.5–2.0 mm. long, brown stellate-puberulent, without glands; petals obovate-oval, rounded, sessile, 8–10 mm. long, brown-stellate without, puberulent-papillate within; stamens 20, the filaments about 1.0–1.5 cm. long, glabrous, not thickened at the base, attached to an inconspicuous androphore about 0.5 mm. long, the anthers 2 mm. long; pistil oblong-fusiform, the stigma sessile, about 3 mm. long, densely white-stellate, the gynophore about 2.5 cm. long; fruit unknown.

Costa Rica; Panama.

BOCAS DEL TORO: Fish Creek Mountains, vicinity of Chiriquí Lagoon, *von Wedel 2235.*

7. CAPPARIS MIRIFICA Standl. apud Woodson & Schery in Ann. Missouri Bot. Gard. 27:311. 1940.

Small trees about 6 m. tall, the branches terete, rather stout, densely brown stellate-tomentose, becoming glabrate; leaves ovate-oblong, rounded or shortly and abruptly acuminate at the tip, deeply cordate and amplexicaul at the base, 15–18 cm. long, 6.0–9.5 cm. broad, pale green and glabrous above, very densely brown stellate-tomentose beneath, the petiole 4–5 mm. long; inflorescence terminal or subterminal, umbelliform at the tip of a filiform, scurfy-stellate, naked peduncle about 40–50 cm. long, apparently few-flowered, the fruiting pedicels 2.5–3.0 cm. long, inconspicuously brown stellate-puberulent; flowers unknown; fruits siliquiform, linear-fusiform, strongly angulate and obviously constricted, 20–30 cm. long, about 8 mm. thick, finely and densely brown stellate-puberulent, the gynophore about 4 cm. long.

Panama.

CANAL ZONE: vicinity of Salamanca Hydrographic Station, Río Pequení, alt. ca. 80 m., *Woodson, Allen & Seibert 1591.*

8. Capparis verrucosa Jacq. Enum. Pl. Carib. 23. 1760.

Capparis laeta HBK. Nov. Gen. & Sp. 5:88. 1821.
Capparis brevipes Benth. Bot. Voy. Sulphur 65. 1844.

Shrub usually 2–3 m. tall, the branches slender, terete, glabrous, with olive-gray bark; leaves very shortly petiolate, obovate-oblong, apex acuminate to obtuse, base obscurely cordate, 4–9 cm. long, 1.5–3.0 cm. broad, firmly membranaceous or subcoriaceous, usually more or less puberulent with simple hairs upon either surface, particularly upon the midrib, infrequently glabrate, the petiole 1–3 mm. long; inflorescence terminal, occasionally in the upper leaf axils as well, corymbose, few-flowered, much shorter than the subtending leaves, the pedicels about 1 cm. long, inconspicuously simple-puberulent; sepals closed in the bud, imbricate in 2 unequal series, coriaceous, reniform, the apex rounded, 4–6 mm. long, glabrous, subtending a low, rim-like gland; petals ovate, obtuse, sessile, 1.2–1.5 cm. long, white, glabrous; stamens about 48, the filaments glabrous, 2.5–3.0 cm. long, not greatly enlarged at the base, the anthers 2 mm. long, attached to an androphore less than 1 mm. tall; pistil oblongoid, about 4 mm. long, glabrous, the stigma depressed, the gynophore about 2 cm. long; fruits subovoid, 3–6 cm. long, densely tuberculate, scarlet or orange, the gynophore 2–3 cm. long.

Southern Mexico to Venezuela.

CANAL ZONE: Alajuela, *Heriberto 64;* forests on dry limestone around Alhajuela, alt. 30–100 m., *Pittier 3449.* DARIÉN: Patiño, on cliffs along the beach, *Pittier 5701.* PANAMÁ: Taboguilla Island, *Miller 2005.*

9. Capparis flexuosa L. Sp. Pl. ed. 2. 722. 1762.

Capparis cynophallophora L. Syst. ed. 10. 1071. 1759, in part.
Morisonia flexuosa L. Amoen. Acad. 5:398. 1760.

Shrubs or small trees usually 2–8 m. tall, the branches relatively stout, more or less flexuose when young, glabrous, with a brownish bark; leaves extremely variable, from linear to broadly obovate, apex acute to rounded, base obtuse to rounded, 4–15 cm. long, 1–6 cm. broad, subcoriaceous, glabrous, pale green, the venation verrucose on both surfaces, the petioles about 5 mm. long; inflorescence terminal, occasionally also in the uppermost leaf axils, corymbosely paniculate, few-flowered, much shorter than the subtending leaves, the pedicels 0.5–1.0 cm. long; sepals close in the bud, imbricate in 2 unequal series, ovate-reniform, rounded at the tip, 7–10 mm. long, coriaceous, glabrous, the internal gland low and rim-like; petals ovate or obovate, 1.0–1.5 cm. long, white or pale pink, glabrous; stamens well over 100, the filaments normally 6–8 cm. long, rarely only about 1 cm. long, glabrous, not enlarged at the base, attached to a disciform androphore about 4 mm. in diam. and less than 0.5 mm. high, the anthers 2 mm. long; pistil oblongoid, 5–7 mm. long, glabrous, the stigma depressed, the gynophore usually about 6 cm. long, rarely only 1 cm. long; fruits very broadly and irregularly siliquiform and somewhat compressed laterally, 4–15 cm. long, 1.5–2.0 cm. broad, glabrous, red or orange, the gynophore 1–9 cm. long.

Fig. 50. *Capparis flexuosa*

Southern Mexico to Venezuela and Peru; southern peninsular Florida and the Antilles.

PANAMÁ: Trapiche Island, Perlas group, common along rocky beaches, alt. 0–15 m., *Allen 2606*.

10. CAPPARIS BADUCCA L. Sp. Pl. 504. 1753.

Capparis frondosa Jacq. Enum. Pl. Carib. 24. 1760.
Capparis triflora Mill. Gard. Dict. ed. 8. no. 10. 1768.
Capparis cuneata DC. Prodr. 1:249. 1824.
Capparis stenophylla Standl. in Jour. Wash. Acad. Sci. 13:437. 1923.

Shrubs or small trees 1–5 m. tall, the branches terete, rather slender, glabrous, with greenish gray bark; leaves strikingly heteromorphic, the lower larger and definitely petiolate, the uppermost congested, markedly smaller, and sessile or subsessile, oblong-elliptic to ovate, obtuse to acuminate, the base acute to obtuse, 6–20 cm. long, 2–7 cm. broad, dark green, glabrous, the midrib elevated above, the petioles 6 cm. long to essentially obsolete; inflorescences of short, slender, few- to several-flowered racemes in the upper leaf axils, shorter than the subtending leaves, the pedicels about 0.5–0.7 mm. long, glabrous; sepals open in the bud,

ovate-trigonal, acute, about 2 mm. long, glabrous, subtending a low, fleshy gland less than 0.5 mm. high; petals broadly oval, sessile, rounded at the tip, 8–10 mm. long, white, glabrous; stamens about 100, the filaments about 1.5 cm. long, glabrous, not thickened at the base, attached to a discoid androphore about 2 mm. in diameter and less than 1 mm. high, the anthers about 1.5 mm. long; pistil oblongoid, 4 mm. long, glabrous, the stigma depressed, the gynophore about 1 cm. long; fruits irregularly oblong-siliquiform, more or less moniliform, 3–7 cm. long, about 5 mm. thick, glabrous, orange-red, the gynophore about 1.5 cm. long.

Southern Mexico to Brazil and Peru; Antilles.

CANAL ZONE: Barro Colorado Island, *Standley 31284, 31298, 31378, 41102, Wilson 34, Frost 106, Maxon, Harvey & Valentine 6822;* Río Pedro Miguel, near East Paraíso, moist forest, *Standley 29945;* vicinity of Gatuncillo, *Piper 5621.* DARIEN: Marraganti and vicinity, alt. 10–200 ft., *Williams 1149.* PANAMÁ: Taboga Island, moist thicket, *Standley 27872.*

11. CAPPARIS **uniflora** Woodson, spec. nov.

Arbor ut dicitur 12 m. alta omnino glaberrima, ramulis crassiusculis cortice griseo bene lenticellato; foliis ellipticis vel obovato-ellipticis apice breviter acuminatis basi late acutis 5–9 cm. longis 2.5–4.0 cm. latis membranaceis supra saturate viridibus subtus valde pallidioribus, petiolis 1–2 cm. longis; floribus solitariis in axillis, foliorum superiorum confertis, pedicellis ca. 2.0–2.5 cm. longis; calycis sepalis ut videntur in alabastro apertis subaequalibus trigono-reniformibus apice rotundatis ca. 3 mm. altis foliaceis glabris glandulam subpyrimidalem carnosam ca. 2 mm. altam subtendentibus; petalis ovalibus rotundatis sessilibus ca. 1.2 cm. longis coriaceis basi cucullatis glabris extus viridibus intus albis; staminibus ca. 28 filamentis inaequalibus 2.5–4.0 cm. longis glabris basi albis apice purpureis in androphoro ca. 1 mm. alto insertis, antheris ca. 3 mm. longis; pistillo oblongoideo ca. 2 mm. longo glabro stigmate plano, gynophoro ca. 2 cm. longo; fructu ignoto.

Trees said to attain 12 m. in height, glabrous throughout, the branches rather stout with glabrous lenticellate bark; leaves elliptic or obovate-elliptic, apex shortly acuminate, base broadly acute, 5–9 cm. long, 2.5–4.0 cm. broad, membranaceous, dark green above, much paler beneath, the petioles 1–2 cm. long; flowers solitary and gathered in the axils of the uppermost leaves, the pedicels about 2.0–2.5 cm. long; sepals apparently open in the bud, subequal, trigonal-reniform, rounded at the tip, about 3 mm. long, foliaceous, each subtending a fleshy, subpyramidal gland about 2 mm. tall; petals oval, rounded, sessile, about 1.2 cm. long, coriaceous, cucullate at the base, glabrous, green without, white within; stamens about 28, the filaments inequal, 2.5–4.0 cm. long, glabrous, white at the base, purple above, inserted on an androphore about 1 mm. long, the anthers about 3 mm. long; pistil oblongoid, about 2 mm. long, glabrous, the stigma flat, the gynophore about 2 cm. long; fruit unknown.

COCLÉ: trail to Las Minas, north of El Valle, alt. 1000 m., May 10, 1941, *P. H. Allen 2460* (Herb. Missouri Bot. Gard., TYPE).

Previously identified as *C. Baducca*, but sharply distinguished by the characters given in the key and descriptions.

12. Capparis ovalifolia R. & P. Fl. Peruv. 4: *t. 432.* 1802.

Capparis avicennifolia HBK. Nov. Gen. & Sp. 5:94. 1821.
Colicodendron avicenniaefolium (HBK.) Seem. Bot. Voy. Herald, 78. 1852.

Shrubs or small trees, the branches terete, relatively slender, densely stellate-canescent; leaves petiolate, oval to oblong-obovate, broadly rounded and minutely mucronulate, cuneate, 4–6 cm. long, 2–3 cm. broad, firmly membranaceous, lustrous and glabrate above, densely stellate-canescent beneath, the petiole about 1 cm. long, densely stellate-canescent; inflorescence terminal, somewhat shorter than the subtending leaves, corymbiform-racemose, bearing several smallish white flowers, densely stellate-canescent throughout, the pedicels about 1 cm. long, the bracts minute, caducous; calyx campanulate, 2.5–3.0 mm. long, the lobes broadly trigonal, about as long as the tube, densely stellate-canescent, each subtending a conspicuous, adnate disk gland of nearly equal length; petals 4, equal, obovate, obtuse, shortly ungulate, 4–5 mm. long, white, glabrate; stamens 20, slightly longer than the petals, the filaments glabrous, inserted upon a low androphore; pistil ovoid, about 3 mm. long, glabrous, the stigmas sessile, the gynophore about 6 mm. long; fruits ovoid-subglobose, about 2.5 cm. in diameter.

Panama to Peru.

DARIÉN: "Isthmus of Darién", *Barclay s. n.*

This species has not been recollected in more than a century since Barclay's visit to Panama. Indeed, it is questionable whether the specimen cited comes from territory at present included within the Republic of Panama, or from the neighboring intendencia of Choco, Colombia.

In addition to the preceding species of *Capparis,* Standley and Steyermark (Fl. Guatemala 4:386. 1946) cite Capparis indica (L.) Fawc. & Rendle, as occuring in Panama. We have seen no Panamanian specimens of this species, which generally resembles *C. odoratissima* but with the calyx open in the bud, but it is quite likely that it occurs in the republic.

5. STERIPHOMA Spreng.

Steriphoma Spreng. Syst. 4: Cur. Post. 130, 139. 1827.

Hermupoa Loefl. Iter Hisp. 307. 1758.
Stephania Willd. Spec. Pl. 2:239. 1799.
Roemera Tratt. Gen. 88. 1802.

Shrubs or small trees, abundantly clothed with orange stellate-pubescence in all parts; leaves alternate, simple, exstipulate; inflorescence racemose, bracteate; sepals concrescent, rupturing into 2–3 irregular lobes at anthesis, somewhat glandular at the base within; petals 4, more or less unequal; stamens 6–8, the filaments attached to a short androphore; pistil borne upon an elongate gynophore, super-

Fig. 51. *Steriphoma macranthum*

ficially 2-celled by the opposed parietal placentas, the ovules numerous, campylotropous; fruit a fleshy dehiscent or indehiscent silique.

1. Steriphoma macranthum Standl. in Jour. Wash. Acad. Sci. 20:183. 1919.

Shrubs or small trees, orange stellate-pubescent in all parts; leaves long-petiolate, ascending, elliptic, narrowly acuminate, base broadly acute, 15–25 cm. long, 5–10 cm. broad, delicately membranaceous, the petioles 6–12 cm. long; inflorescence racemose, many-flowered, the peduncle rather stout, nearly equalling the subtending leaves, the pedicels strongly ascending, 3–4 cm. long; calyx declinate, about 1.7–2.0 cm. long; petals apparently about 2.5 cm. long; stamens 8, the filaments 6–8 cm. long, strongly ascending, attached to an androphore less than 0.5 mm. long; pistil oblongoid, about 5 mm. long, the gynophore about equaling the staminal filaments; fruit unknown.

Panama.

DARIÉN: forests around Pinogana, *Pittier 6561.*

CRUCIFERAE

BY REED C. ROLLINS

Annual, biennial, or perennial herbs; leaves without stipules, alternate, simple or compound, entire to variously lobed or dentate; inflorescence racemose, ebracteate, or the lower flowers subtended by leaf-like bracts; flowers perfect, regular; sepals 4, free, alternating with petals, non-saccate or the outer pair slightly saccate; petals 4, free; stamens usually 6 in two whorls, outer stamens 2, unpaired, usually shorter than paired inner 4; ovary superior, 2-celled with the cells separated by a replum, or rarely 1-celled; style 1, stigma 2-lobed to entire; fruit a silique, dehiscent or rarely indehiscent.

The Cruciferae are distributed primarily in the temperate latitudes of both hemispheres. The family is sparsely represented in strictly tropical areas. Panama has but few genera and species. Some weedy members of the family not now known from Panama are to be expected in or near cities or agricultural areas.

a. Siliques linear, many times longer than broad, 1 cm. or more in length.
  b. Siliques dehiscent by valves which open the fruit nearly its entire length.
    c. Leaves compound; replum margins thickened .... 1. Cardamine
    cc. Leaves simple; replum margins not thickened.
      d. Petals white, minute, less than 5 mm. long .... 2. Romanschulzia
      dd. Petals yellow, conspicuous, more than 5 mm. long .... 3. Brassica
  bb. Siliques without linear valves, jointed and disarticulating near middle .... 4. Cakile
aa. Siliques short, usually not more than 3 times longer than broad, less than 6 mm. long.
  b. Siliques terete, not notched at apex .... 5. Rorippa
  bb. Siliques strongly flattened at right angles to the narrow replum, notched at apex .... 6. Lepidium

Fig. 52. *Cardamine ovata*

1. CARDAMINE L.

CARDAMINE L. Sp. Pl. 654. 1753; O. E. Schulz in Bot. Jahrb. 32:280–623. 1903.

Perennial or less frequently annual herbs, pubescent with simple trichomes or glabrous; stems leafy, the leaves petiolate and usually pinnately compound; inflorescence racemose, ebracteate or the lower flowers bracteate; petals spatulate to obovate, white to pink; siliques linear, compressed parallel to the replum, dehiscent by linear, often elastic, valves, tapering at apex to a cylindrical style; stigma usually 2-lobed; seeds emarginate or rarely very narrowly winged.

Cardamine and *Dentaria* are most easily recognized among other linear-podded crucifers by the nature of the opening in the siliques after the valves have dehisced. In these two genera, the replum margin is comparatively thick and extends laterally from the margins to reduce the area covered by the valve. Thus the silique has a window-like opening. In other crucifers of the same general relationship with linear siliques, the valves cover the entire flattened side of the silique.

1. CARDAMINE OVATA Benth. Pl. Hartweg. 158. 1839.

Perennial with an underground scaleless rhizome from which the stems arise at short intervals; stems erect or slightly decumbent at base, weak, simple to sparsely branched, striated, glabrous below, glabrous to sparsely pubescent above, 2–6 dm. high; leaves all cauline; petioles glabrous, 2–7 cm. long; leaflets 3–5, elliptical to narrowly ovate, obtuse at apex, cuneate at base, irregularly crenate to shallowly toothed, mucronate, 2–6 cm. long, 1–3 cm. wide, sparsely pubescent with simple trichomes; inflorescence bracteate below, bracts absent above; sepals oblong, pubescent, scarious-margined, 2–3 mm. long, inner pair non-saccate, outer pair slightly saccate; petals white, spatulate to ligulate, 6–10 mm. long; fruiting pedicels divaricately ascending, straight, sparsely pubescent, 1–2.5 cm. long; siliques divaricately ascending, 3–6 cm. long, styles 1–3 mm. long; seeds wingless, oblong, 2–3 mm. long, ca. 1.5 mm. wide.

Costa Rica southward to Peru.

CHIRIQUÍ: Bajo Chorro, Boquete, *Davidson 201;* vicinity of Bajo Chorro, *Woodson & Schery 638;* trail from Bambito to Cerro Punta, *Allen 312;* valley of upper Río Chiriquí Viejo, *G. White 95;* Volcán de Chiriquí, *Davidson 1028, Killip 3581, Pittier 3123.*

2. ROMANSCHULZIA O. E. Schulz

ROMANSCHULZIA O. E. Schulz in Bot. Jahrb. 66:99. 1934.

Annual, biennial, or perennial herbs; pubescence simple; stems single from the base, often coarse, usually branched above, glabrous or pubescent; basal leaves present or absent; cauline leaves sessile, auriculate, sagittate, usually longer than the internodes; inflorescences greatly elongated, terminating many branches as well as the main stem; flowers mostly numerous, small; sepals caducous or at least early deciduous, non-saccate; petals narrow, spreading at anthesis; stamens equal or nearly so, mostly spreading at anthesis, filaments enlarged at base; nectar-glands

Fig. 53. *Romanschulzia costaricensis*

mostly well developed, surrounding or at least subtending all stamens; siliques terete to slightly flattened parallel to replum, erect, widely spreading or deflexed, stipitate to nearly sessile; seeds wingless, plump to somewhat flattened, uniseriate to biseriate; cotyledons incumbent to accumbent.

A single species occurs in Panama.

1. ROMANSCHULZIA COSTARICENSIS (Standley) Rollins in Contrib. Dudley Herb. Stanford Univ. 3:219. 1942.

Sisymbrium costaricense Standley in Jour. Wash. Acad. Sci. 17:251. 1927.

Perennial; stems single from the base, glabrous, coarse, branched, 1–1.5 m. high; leaves sessile, oblong to lanceolate or the lower often oblanceolate, acute to nearly obtuse, 6–15 cm. long, 1–3 cm. wide, greenish above, dull beneath, auriculate-clasping, upper smaller and more attenuate than the lower, auricles rather rounded; inflorescences of main stem and branches greatly elongated, very lax; sepals greenish, sometimes purplish-tipped, non-saccate, 2.5–3 mm. long, 1.5 mm. wide; petals narrowly oblong, white to creamy-white, about 2–2.5 mm. long, 0.5 mm. or less in width; filaments 1.5–2 mm. long, anthers about 1.5 mm. long; glandular tissue subtending all filaments, surrounding those of the single stamens; pedicels spreading at right angles to rachis or very slightly ascending, straight or nearly so, glabrous, 3–8 mm. long; mature siliques terete, spreading at right angles to rachis, straight, glabrous, 2–3 cm. long, about 1 mm. broad, shortly stipitate to nearly sessile, gynophore less than 1 mm. long; seeds uniseriate, oblong, wingless, about 1 mm. long, fairly plump; cotyledons accumbent.

Costa Rica and Panama.

CHIRIQUÍ: above El Boquete, *Pittier 3058;* Bajo Chorro, Boquete, *Davidson 447;* valley of the upper Río Chiriquí Viejo, *G. & P. White 1.*

3. BRASSICA L.

BRASSICA L. Sp. Pl. 666. 1753; O. E. Schulz, Pflanzenr. IV, 105, Heft 70:21-84. 1919; Bailey, Gentes Herb. 1:53-108. 1922; ibid. 2:211-267. 1930.

Annual or biennial herbs, glabrous or pubescent with simple trichomes; stems usually single from the base, branched above; leaves sessile or petiolate, simple to somewhat divided; inflorescence racemose, ebracteate; sepals oblong to slightly broader, outer pair slightly saccate; petals yellow, spatulate; siliques linear, slightly flattened parallel to replum, usually sterile above and forming a tapering beak; seeds globose or nearly so, wingless; cotyledons conduplicate.

There are no species of *Brassica* native to the Western Hemisphere, but several species and their varieties are grown as vegetables. The two following species are found in Panama as introduced weeds in fields and waste places.

Called *Mostaza* or *Mostacillo,* and cultivated for its edible leaves.

a. Upper cauline leaves sessile and auriculate; beak and style of mature siliques 1–2 cm. long .... 1. B. CAMPESTRIS
aa. Upper cauline leaves petiolate; beak and style of mature siliques ca. 3–5 mm. long .... 2. B. INTEGRIFOLIA

1. Brassica campestris L. Sp. Pl. 666. 1753.

Annual; stems single from base, glabrous, glaucous, usually branched above, 4–10 dm. high; lower leaves interrupted, often short-petiolate with the expanded base clasping the stem, obovate, 1–2 dm. long, 3–8 cm. wide; upper leaves sessile and clasping, entire or nearly so, oblong, obtuse to rounded at apex; flowers 7–10 mm. long; fruiting pedicels divaricate, 1–2 cm. long, glabrous; siliques divaricate to divaricately ascending, glabrous, 3–5 cm. long, nearly terete to slightly flattened parallel to replum, valves 1-nerved to middle or above; beak and style 1–2 cm. long; seeds dark brown, globose, ca. 1 mm. in diameter.

CHIRIQUÍ: vicinity of El Boquete, *Maurice 751.*

2. Brassica integrifolia (Willd.) Rupr. Fl. Ingr. 1:96. 1860.

Sinapis integrifolia Willd. Hort. Berol. *pl. 14.* 1803.

Annual, glabrous, usually glaucous; stems single from the base, branched above, 5–10 dm. high; lower leaves long-petioled, blade irregularly dentate, oval to broadly obovate, obtuse; upper leaves narrower and shorter-petioled, acute to more or less acuminate, becoming almost entire above; flowers yellow, 7–10 mm. long; infructescences much elongated; pedicels divaricately ascending, glabrous, about 1 cm. long; siliques erect or ascending, 2–3 cm. long, valves with a prominent midvein, beak and style 3–5 mm. long; seeds oval, dark brown, ca. 1 mm. in diameter.

Brassica integrifolia is very closely related to *B. juncea* and may not merit the status of a species. Plants usually determined as *B. integrifolia* have shorter, less torulose siliques and shorter beaks than *B. juncea.* Also, the leaves are irregularly doubly dentate rather than notched as in *B. juncea.*

PANAMÁ: between Corozal and Pedro Miguel, *Cowell 402;* around Culebra, *Pittier 4067.*

4. CAKILE Mill.

Cakile Mill. Gard. Dict. ed. 4, 1:118. 1754; O. E. Schulz, Pflanzenr. IV, 105, Heft 84:18-28. 1923.

Annual or biennial herbs, succulent; stems intricately branched, fairly stout, decumbent; leaves fleshy when fresh, entire to nearly pinnate, petioled or sessile, never clasping; inflorescence racemose, ebracteate; flowers white to purplish, petals not conspicuous; infructescence elongated; pedicels thick; siliques indehiscent, composed of two joints which disarticulate freely at maturity; lower joint turbinate, 1-seeded, upper joint gradually tapering to a beak; seeds oblong, wingless.

1. Cakile lanceolata (Willd.) O. E. Schulz in Urban, Symb. Antill. 3:504. 1903.

Raphanus lanceolatus Willd. Sp. Pl. 3:562. 1800.

Annual; stems coarse, decumbent, 2–6 dm. long, glabrous; leaves with a very slender petiole, narrowly elliptical to linear-oblanceolate, dentate, acute to obtuse, 3–6 cm. long, glabrous; flowers small, ca. 5 mm. long; petals white; fruiting

pedicels divaricate, thick, 2–4 mm. long; siliques linear, lower joint nearly cylindrical, 3–4 mm. in diameter, 1 cm. or less in length, obscurely nerved; upper joint lanceolate, subterete to slightly flattened toward apex, 1.5–2.5 cm. long; seeds oblong, wingless, plump, ca. 3.5 mm. long, 1.5 mm. wide.

West Indies, South Carolina coast southward to Panama.

COLÓN: along the beach and near sea level, vicinity of Viento Frio, *Pittier 4113*.

5. RORIPPA Scop.

RORIPPA Scop. Fl. Carn. ed. 1, 520. 1760.

Annual or perennial herbs, glabrous or pubescent with simple trichomes; leaves sessile or petioled, simple to deeply lobed; inflorescence racemose, ebracteate, terminating all the upper branches; flowers small, petals yellow or rarely white; infructescence usually somewhat elongated; siliques short, rarely up to 4 times longer than broad, usually much shorter, terete, plump, valves nerveless; style short, stigma unexpanded.

1. RORIPPA ISLANDICA (Oeder ex Murray) Borbás, Balat. Tav. Part. 392. 1900.
Sisymbrium islandicum Oeder ex Murray in Nov. Com. Gött. 3:81. 1773.

Annual or possibly perennial; stems glabrous, striate, branched above, 3–6 dm. high; leaves broadly oblanceolate, obtuse, prominently veined, glabrous, erose or irregularly dentate, lower leaves petioled and often somewhat lobed, 5–10 cm. long, 1–2 cm. wide; upper leaves sessile or short-petioled, lobed or merely erose-margined, less than 5 cm. long; inflorescence congested, elongating in fruit; flowers ca. 2 mm. long, petals yellow; fruiting pedicels divaricate, 2–4 mm. long; siliques terete, ca. 2 mm. in diameter, 3–5 mm. long, glabrous; styles less than 1 mm. long; seeds small, less than 0.5 mm. broad, wingless.

Rorippa islandica is an introduced weed in Panama. The species is native to a wide area in northern North America and northern Europe and is composed of several varieties. It is not certain whether the Panama plants represent one of the European or one of the North American varieties of the species.

BOCAS DEL TORO: along railroad, Changuinola Valley, *Dunlap 392*.

6. LEPIDIUM L.

LEPIDIUM L. Sp. Pl. 643. 1753; C. L. Hitchcock in Madroño 3:265-320. 1936; ibid. 8:118-143; Lilloa 11:75-134. 1945.

Annual or perennial herbs, glabrous or pubescent with simple trichomes; leaves entire to bi- or tripinnate, sessile or the lower petiolate; inflorescences terminating the upper branches, racemose, congested in flower, elongating in fruit; flowers small; petals lacking or mere vestiges or up to 3 mm. long, white to sulphur-yellow; stamens 2, 4 or 6, anthers nearly orbicular; siliques strongly flattened contrary to the narrow replum, usually rounded, glabrous to hirsute, apex scarcely

notched and barely winged to deeply notched and prominently winged; styles present or absent; seeds 2, one in each locule; cotyledons accumbent to incumbent.

1. Lepidium virginicum L. Sp. Pl. 645. 1753.

Annual; stems freely branched, 1.5–6 dm. high, sparsely pubescent above with minute trichomes; lower leaves irregularly toothed to pinnately divided; upper leaves oblanceolate, acute, irregularly toothed or serrate to almost entire, cuneate at base, becoming smaller upward; racemes numerous and many-flowered; sepals glabrous to sparsely pubescent, ca. 1 mm. long; petals white, slightly exceeding the sepals; stamens usually 2; fruiting pedicels terete, divaricately ascending to spreading at right angles, glabrous or nearly so, somewhat longer than the fruits; siliques glabrous, orbicular to slightly longer than broad, 2.5–3.5 mm. long, shallowly notched at apex; style included in the shallow notch; seeds wingless; cotyledons accumbent.

Typical *Lepidium virginicum* is native to southeastern North America and the West Indies. The species as a whole has many varieties and is widespread in North America and is found in parts of South America. As a weed, it is even more widely distributed. The following collection belongs to var. *typica.*

Chiriquí: pasture weed around Alto Lino, vicinity of El Boquete, *Maurice 712.*

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A DICOTYLEDONOUS WOOD FOUND ASSOCIATED WITH THE IDAHO TEMPSKYAS

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In a recent number of this journal, a series of new interpretations and a summary of our knowledge of the fossil fern *Tempskya* were presented by Andrews and Kern ('47). As a part of their contribution, they described the other plant remains that had been found associated with *Tempskya* in the Cretaceous beds of Idaho. Representatives of the Bennettitales and of the Coniferales were described, and mention was made of a dicotyledonous wood that occurred with these fossils at the Wayan, Idaho, site. This dicotyledonous wood will be described in the present paper in the hope that it will add something to our meager knowledge of the type of plant that lived with, or in the vicinity of, these most peculiar fossil ferns.

The wood specimen was collected near Wayan, Idaho, the site being just east of the Wayan post-office. The source rock is the Wayan Formation which is listed by Wilmarth ('38) as Upper Cretaceous on the basis of the work of Read and Brown ('37). Lower Cretaceous age is also suggested by Wilmarth, and thus it is apparently not possible at the present time to put the formation in its proper place in the Cretaceous without a feeling of uncertainty. The wood is silicified, or partially so, but as can be seen from the photographs, sufficient structure has been preserved so that it is not difficult to make out most of the important features. The thin sections were prepared in the laboratory of Dr. H. N. Andrews and sent to the author for identification. The slides from which the description has been made are Nos. 1482, 1483, and 1484, of the Henry Shaw School of Botany Collections, Washington University, St. Louis.

After considerable study of these slides and of the woods with similar structure to be found in the Harvard Wood Collection, it became evident that, on the basis of the available comparative material, it would be impossible to assign this fossil wood to any living genus or species. At this point Professor I. W. Bailey suggested

that this fossil wood appeared to be similar to a wood he described from the Upper Cretaceous (Colorado Group) of Arizona. A portion of the type specimen of this Arizona fossil was obtained from the U. S. National Museum through the courtesy of Dr. Roland W. Brown and thin sections were prepared from this specimen. *Paraphyllanthoxylon arizonense* Bailey was then compared with the Idaho dicotyledonous wood.

The structure of these two woods is remarkably similar, and, while it must be admitted at the outset that they are not identical, it would be extremely difficult to justify the assignment of this new wood to a genus other than *Paraphyllanthoxylon*. The Idaho wood differs from *Paraphyllanthoxylon arizonense* Bailey in several of its characters but none of these fall outside of the limits set by Professor Bailey in his definition of this form-genus (Bailey, '24).[1] The vessels in the Arizona fossil are fewer in number and larger in cross-section, and the intervascular pitting is inclined to be more abundant, approaching at times a hexagonal pattern. Further, the rays in *P. arizonense* are wider and higher, and the individual cells are more radially elongate. The magnitude and the nature of these variations are well within the range of variability found in individuals of many living species, and thus the differences in the two fossils might be accounted for on the basis of the part of the tree from which the specimen was derived, differences in growth rate, etc. In spite of this, however, it seems appropriate, because of these differences, to describe this new wood as a new species with the hope that the true relationship of these two fossils will be demonstrated in the future as the result of an increasing understanding of fossil woods.

The Idaho fossil wood may be described as follows:[2]

Paraphyllanthoxylon idahoense sp. nov.

Growth Rings:

While it was at first thought that there was some reason to believe that growth rings might be present (fig. 7) it now seems clear that the one isolated area in question is simply a patch of radially narrow septate fibers such as often occur in a number of woods (e. g., *Mespilodaphne sassafras* Meissn.—Lauraceae).

Vessels:

Average diameter: 100 μ; range 60–160 μ. *Average length:* approximately 500 μ. *Arrangement:* wood diffuse, porous; vessels solitary and in short multiples of 2 or 3, occasionally clusters of 3 or 4 (figs. 1 and 2). *Perforation plates:* exclusively simple; angle of end wall oblique to transverse (fig. 6). *Intervascular pitting:* alternate, abundant, circular to elliptical, rather large, i. e. 10–12 μ; orifice slit-like (fig. 6). *Vessel-parenchyma*

[1] Professor Bailey states that the genus was created "for the reception of dicotyledonous woods having combinations of anatomical characters such as occur in mature stems of *Phyllanthus emblica* L., and other structurally similar representatives of the Phyllanthoideae."

[2] The features used are those suggested by Tippo ('41), and the terms are used as defined by the Committee on Nomenclature, International Association of Wood Anatomists ('33).

pitting: elongate-oval (as in the Flacourtiaceae), at least in part (particularly on the erect ray cells). *Tyloses:* abundant, multiple; tightly packed in all, or nearly all, vessels; not sclerotic (fig. 4).

Xylem Parenchyma:

Very sparsely paratracheal (vasicentric). Crystal-bearing strands diffuse *if present.* Although some areas suggest the presence of crystal-bearing parenchyma strands (fig. 4) this could not be conclusively demonstrated. These structures may indicate resiniferous septate fibers or may simply be a product of the degradation of the cell wall.

Xylem Rays:

Abundant; mostly multiseriates. Cells partially filled with some ergastic material (probably phenolic compounds). Multiseriate rays 2–4 cells wide, most of the cells being procumbent with the marginal cells usually erect (fig. 3). Uniseriate rays usually contain a mixture of erect and procumbent cells (fig. 3). Structures suggesting the presence of crystals are occasionally observed.

Fibers:

Septate fiber-tracheids throughout (fig. 5).

Assuming the septate fibers, abundant tyloses, and the nature of the perforation plate to be constant features in the older secondary xylem of the fossil species, the number of families to which it could be related is comparatively few. Study of the woods of the families thus selected revealed a number of genera that contained species closely similar to the fossil, none of which, however, were identical. The similarities and differences between the fossil and these living species are summarized in Table I. Only one species of each genus is listed although in the case of *Canarium* and *Beilschmiedia* there are other species that are equally similar.

Of the six families included in the table, the fossil finds its best counterparts in the Anacardiaceae, Burseraceae, and the Euphorbiaceae. The absence of radial gum ducts in the fossil, however, reduces the possibility of it being either a *Koordersiodendron* or a *Garuga,* although in most other features the similarities are quite striking. It is, of course, possible that the fossil had gum ducts and, by chance, none are contained in the specimen studied. This possibility should certainly be recognized, but it is obvious that it is impossible to go beyond this point and still justify one's methodology.

Bridelia minutifolia Hook. (Euphorbiaceae) possesses a number of features in common with the fossil, and its ray type may not be too dissimilar to be an ontogenetic phase of the fossil ray type. The same applies to *Phyllanthus emblica* L., but in both cases it is evident that the living wood is by no means identical with that of the fossil. The Lauraceous forms are quite similar but the inflated secretory cells in the rays eliminate these from our consideration. *Kirkia acuminata* Oliver (Simarubaceae) may be rejected because of its ray type, and while the rays of

TABLE I

A COMPARISON OF THE FOSSIL WOOD WITH SIMILAR LIVING SPECIES

Possible Relative	Vessels					Fibers	Xylem parenchyma	Xylem rays	Other Features
	Approximate length (microns)	Form and arrangement	Perforation plate	Intervascular pitting	Vessel-ray pitting				
ANACARDIACEAE									
Koordersiodendron pinnatum Merr.	480	X[1]	X	X	X	X	X[2]	—[3]	Radial gum ducts present; ergastic material in the rays and fibers very similar to that of the fossil
Schinopsis balansea Engl.	300	—	X	X	X	X[4]	—	—	Radial gum ducts present
Mauria simplicifolia DC.	300	—	X	X	X	X[4]	X	—	Abundant strands of crystal-bearing parenchyma present
BURSERACEAE									
Garuga pinnata Roxb.	310	—	X	X	X	X	X	X	Radial gum ducts present
Canarium rufum Benn.	330	—	X	X	X	X	X	—	Radial gum ducts present
EUPHORBIACEAE									
Phyllanthus emblica L.	480	—	X	X	X	X	X	—	Tyloses in vessels infrequent
Bischofia javanica Blume	420	X	X	X	X	—[5]	X	—	Walls of ray cells "beaded"
Bridelia minutifolia Hook.	480	X	X	X	X	X	X	—	Tyloses in vessels infrequent; strands of crystal-bearing parenchyma present
LAURACEAE									
Beilschmiedia roxburghiana Nees	410	—	X[6]	X	X	X	X[2]	—	Secretory cells present
Mespilodaphne sassafras Meissn.	360	X	X	X	X	X	X[2]	—	Secretory cells present
SIMARUBACEAE									
Kirkia acuminata Oliver	350	X	X	X	X	X	X	—	
VERBENACEAE									
Petitia domingensis Jacq.	320	—	X	X	X	X	X	X?	

[1] (X) signifies that structure is identical with fossil.
[2] Paratracheal parenchyma more abundant than in fossil.
[3] (—) signifies that structure differs from the fossil.
[4] Not all fibers are septate.
[5] Libriform septate fibers.
[6] Occasionally scalariform.

Petitia domingensis Jacq. (Verbenaceae) are more similar, the structure and arrangement of the vessels throw doubt on this form.

Some of the characteristics of the fossil can be found in families other than those listed above. For example, in the family Urticaceae the genera *Laportea* and *Pipturus* have abundant tyloses in the vessels, simple perforation plates, and the fibers are all septate. Numerous other features of the woods (storied cambium, wood parenchyma distribution, etc.) exclude the possibility of assigning the fossil to any of these families, and the inclusion of these and like forms in the table would have contributed nothing to our understanding of the fossil so they were omitted. It is clear, from the table and from these remarks, that this fossil has a combination of characters which can be similarly approximated in a number of dicotyledonous families. In view of this it appears unwise to suggest any specific family to which the fossil should be assigned, but it should be noted that the Anacardiaceae, Burseraceae, and the Euphorbiaceae represent the best possibilities.

All the species listed in the table are tropical or sub-tropical forms, but they represent both hemispheres and a variety of habitats. *Schinopsis* is found in swampy river bottoms, *Mauria* in highland areas; *Petitia* is confined to the West Indies, *Bischofia* to the Indo-Malayan region, etc. Little light, therefore, is thrown on the possible habitat of this cretaceous dicotyledon by the ecological and phytogeographical relations of the similar living species, although the implication is that it was not a temperate or cold temperate form. Hence, the identity, real affinity, and the greater part of the significance of this wood remain obscure, but the knowledge of the existence of a dicotyledon of this type among the remains of *Tempskya* is an interesting addition to our rather scant collection of facts regarding the associates of this extinct fern type.

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Explanation of Plate

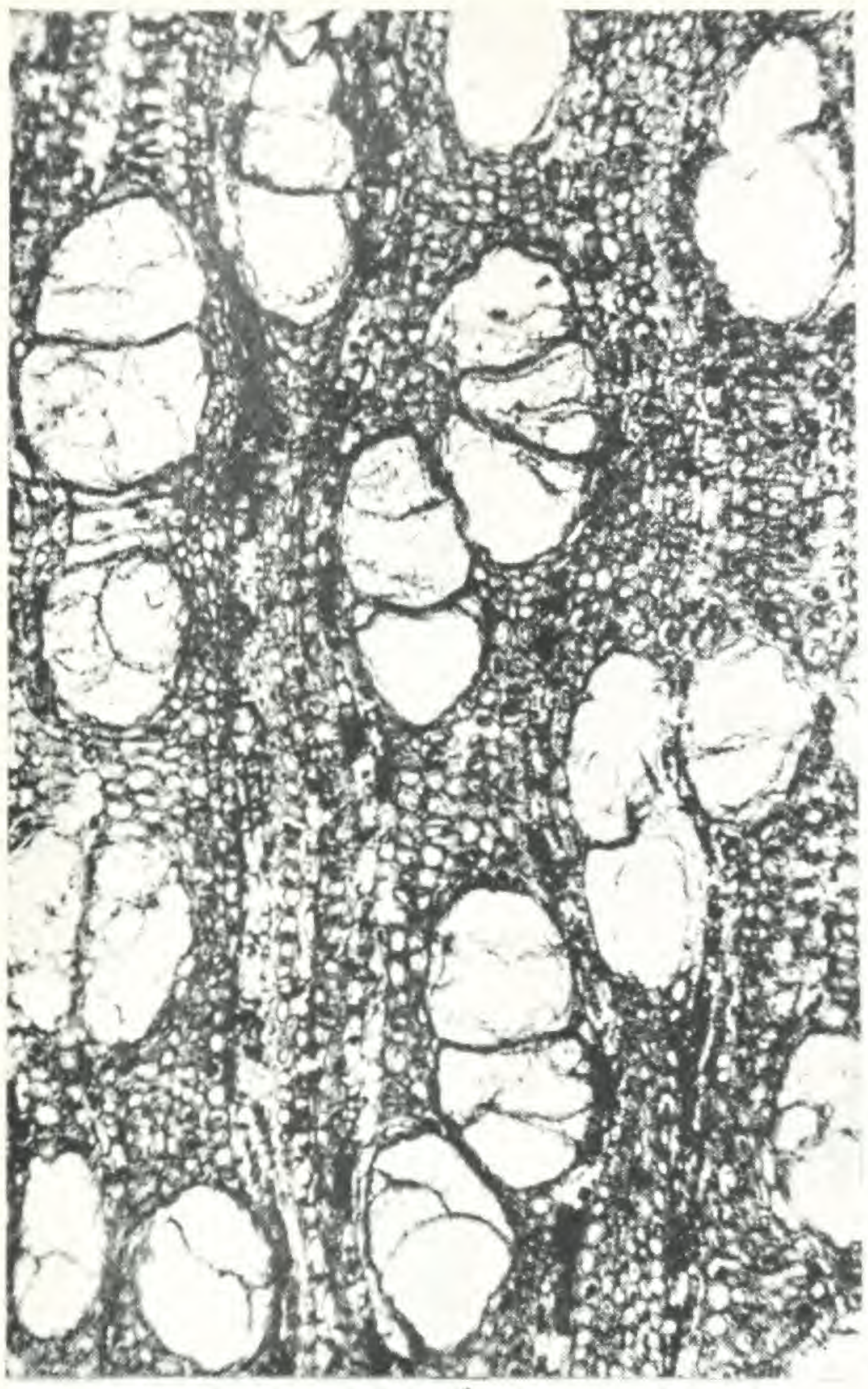
PLATE 1

Paraphyllanthoxylon idahoense

Figs. 1 and 2. Transverse sections showing the form and arrangement of the vessels and fibers. From slide No. 1482, × 100.

Fig. 3. Tangential section showing ray structure. From slide No. 1483, × 100.

Fig. 4. Radial section showing the abundant tyloses in the vessels and the questionable crystal-bearing parenchyma strands. From slide No. 1484, × 100.



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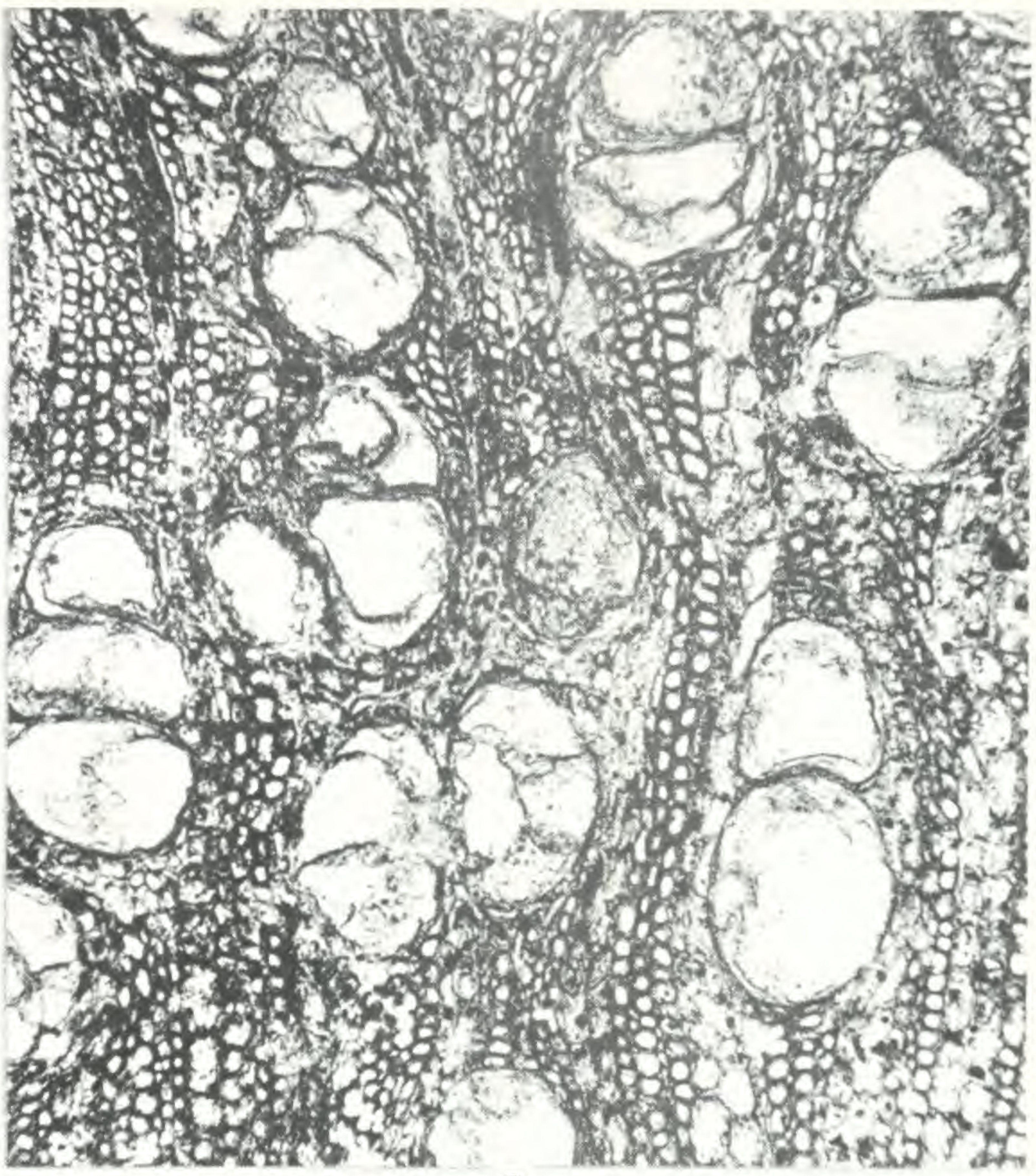

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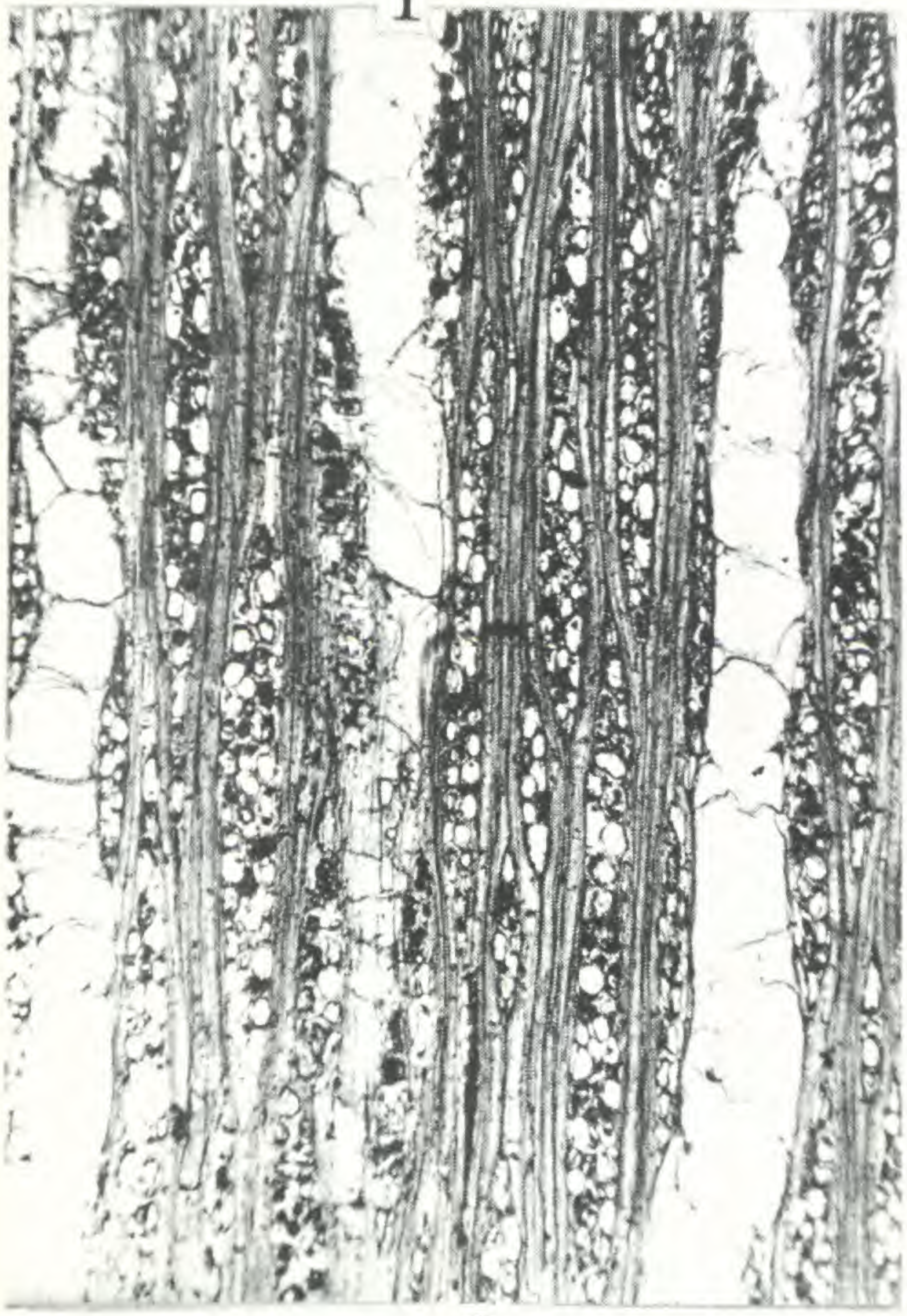

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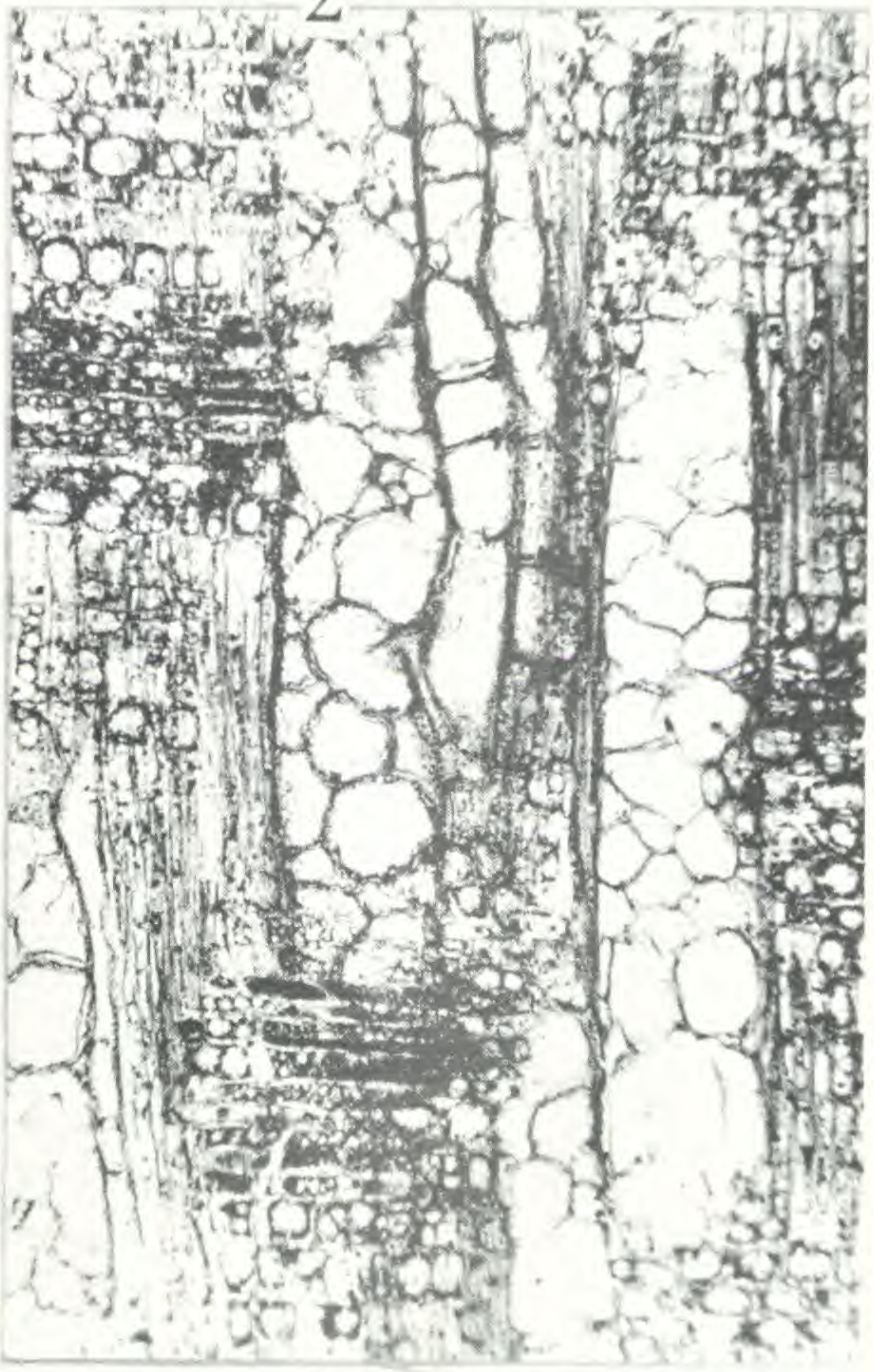

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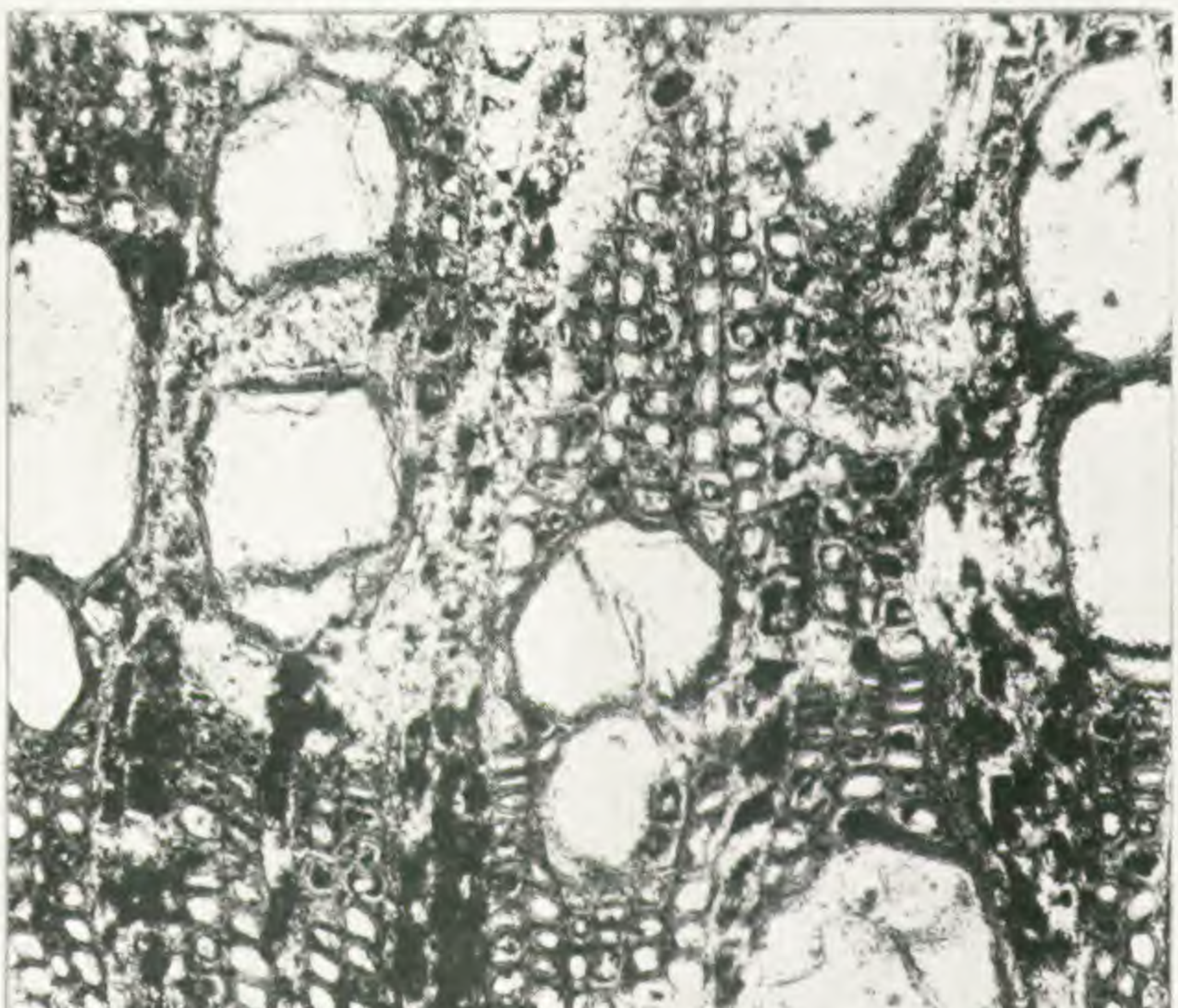
SPACKMAN—PARAPHYLLANTHOXYLON IDAHOENSE

5

6



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SPACKMAN—PARAPHYLLANTHOXYLON IDAHOENSE

Explanation of Plate

PLATE 2

Paraphyllanthoxylon idahoense

Fig. 5. Tangential section showing septate fibers and the details of the multiseriate rays. From slide No. 1483, × 150.

Fig. 6. Tangential section showing the details of the characteristic vessel type. From slide No. 1483, × 150.

Fig. 7. Transverse section showing the patch of radially narrow fibers which was at first thought to be part of a growth ring. From slide No. 1482, × 150.

THE USES OF HEVEA FOR FOOD IN RELATION TO ITS DOMESTICATION

R. J. SEIBERT[1]

The domestication of plants involves many factors about which there is little direct information. Many of our most useful plants originated so long ago that we do not know their exact geographical origin or the plant or plants from which they were derived. Modern man, in his short span of keeping accurate records, can turn to few examples which offer the complete history of the domestication of a plant. *Hevea* is one plant which is being domesticated in a modern world by reason of its recent value as the world's most economical rubber producer. Its history is so short as scarcely to have changed the plant from its role as a wild jungle tree; yet it will serve as an example from which we may gain further insight into ancient plant domestication.

How do plants become domesticated? To the uninitiated this question may seem too simple for serious consideration. But if it is so simple why are our best research men still in a controversial quandry regarding the origin of maize and most of our other cereals? We may say that plants become domesticated by man through countless generations of cultivation and conscious or unconscious selection of the best-yielding or most adaptive individuals for further propagation. As far as it goes, this may be true but it does not take into account the effects that wild forage animals may have had upon domestication. Little is known of the effect of gradual and catastrophic changes in ecology caused either by man or nature. Seldom can all of the possible factors concerning seed and plant distribution be accurately reconstructed. We must contend with such difficult factors as long-past chance hybridizations and mutations in a plant's history of domestication.

The domestication of a wild plant is brought about by its being taken from its native habitat and reproduced for successive generations under man-modified conditions. Some species have been cultivated in different regions for different reasons at different times. What has happened when two or more of these closely related strains have been brought together? Evidence of such appears in maize literature (Anderson, '46). There are distinct strains of flax, one for seed oil, the other for fibre, certainly an important factor to be considered. The nature of a wild plant may become so changed through the long and complicated process of domestication that it can no longer survive without the aid of man. What would become of the domesticated plants which must rely on man for survival and without which man could not survive?

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How has *Hevea* become domesticated? As a rubber-producing plant, it was taken from the lower Amazon valley to the Far East, seventy-one years ago, into a completely new environment without its indigenous diseases and pests. *Hevea* is a tree crop requiring about ten to fifteen years from seed germination to proven optimum rubber yield. Through selective seed propagation and vegetative budding the average annual yields of seedling trees have been increased from about 350 pounds per acre to above 1500 pounds for bud-grafted trees. This is a remarkable improvement. But, one can scarcely call *Hevea* a highly domesticated plant when comparing its generations of cultivation with those of potatoes or the cereals.

The story of *Hevea* domestication has been often repeated in literature during the past few years. Its most recent chapter concerns the return of the tree to its original home (back to its indigenous diseases and pests) for the development of a Latin American rubber industry through the cooperative sponsorship of the U. S. Department of Agriculture and various Latin American countries (Brandes, '47). This is not the entire history of domestication through which *Hevea* has passed and is passing. Nor is its domestication wholly concerned with a basis of drop-by-drop rubber latex yield from the incised bark.

The domestication of a semi-wild *Hevea* as a food source also must be taken into consideration. There are indications that in its Amazonian home the *Hevea* tree may first have been known to the pre-Columbian aborigine as a nut tree. Probably from acquaintance with *Hevea* as a source of food, the Indian in time learned that certain of these trees produced, through injury to the bark, a substance which could be made into waterproof objects. No doubt one of these objects at some time fell into the fire and the material was seen to burn readily. From this he may have learned that the latex when placed in smoke would coagulate rapidly into a more durable material than when allowed to coagulate naturally. This substance, latex, in its coagulated form, rubber, was destined to overshadow the trees' local value and use for a food.

The celebrated Amazonian plant collector, Richard Spruce, gives the following account, quoted by Bentham (1854):

> Siphonia [Hevea].—This genus seems abundant throughout the Amazon and its tributaries, but not all the species yield caoutchouc (or Xeringue, as it is here called) of good quality. . . . The wood in all is soft, soon decaying. The seeds are an excellent bait for fish. Macaws eat them greedily, but to man and quadrupeds they are poisonous in a fresh state. The Indians on the Uaupés render them eatable in this way: after being boiled twenty-four hours, the liquor is strained off, and the mass that remains has something the colour and consistence of rice long boiled. Eaten along with fish it is exceedingly savoury.
> —R. Spruce, MS.

Baldwin ('47) has confirmed the use of *Hevea* seeds for food by the Indians along the Río Negro. It appears also that the seeds of *Cunuria,* a genus closely allied to *Hevea* (and reputed to have hybridized with it), are prepared and eaten by the Indians of the same general region according to Spruce, as reviewed by Baldwin and Schultes ('47).

The pre-Columbian ancestry of both the Carib and later the Arawak Indians inhabiting the great Amazon tributary, the Río Negro, indicates several centuries

of river transportation and primitive agriculture to have existed within the Amazon valley (Radin, '42) and that, furthermore, intercourse existed between the Río Negro and the Orinoco drainage via the Casiquiare. It is becoming evident that a number of plants, of which I feel the "Peach-palm," *Guilielma Gasipaes* (HBK.) Bailey, may prove to be the classic example, may have been distributed from their native homes on the eastern slopes of the Andes through the Amazon valley (Seibert, '47). By way of the Río Negro and Orinoco they eventually became introduced through the West Indies to Central America. As in *Guilielma,* where seed viability lasts for a long time and where growth requirements are not so exacting, a distribution of this sort might quite likely have been carried on by the Indians. Furthermore, *Guilielma* was and is a more important tree in the economy of these Indians than is usually realized. Its fruit is a source of abundant and nutritious food; its wood furnishes one of the finest materials for bows and arrow-points known; its spines make good needles; its leaves, a usable thatch; and the heart of the palm, an excellent food.

In the case of *Hevea,* seed viability lasts only a few days, or at most a few weeks when specially packed. Although establishment of the seedlings is extremely difficult under all but the best of conditions, nevertheless within the Amazon valley itself *Hevea* was and is often transplanted from jungle to doorstep by many an Indian. As a food source in that region it was an important plant where native food plants are exceedingly rare, but it probably was not worth the effort transporting it to regions where food was no such problem as on the Río Negro. As a rubber-producing plant the Indian, in all probability, relied not on *Hevea* but on *Castilla,* which for his needs and crude methods of tapping was far superior. *Castilla* inhabited Central America, the West Indies, and the Amazon valley, so he had no need for transporting a rubber plant—or did he have something to do with the distribution of *Castilla* as well?

Schultes ('45), from individual observations in the Río Negro region, confirms the evidence from herbarium material that this region of the Amazon valley contains more species of *Hevea* and with greater variability within species than any other region thus far known. Transportation being difficult except along streams, collections from that area have largely been obtained from camp-sites, the edges of villages, and from clearings easily accessible. It is quite likely that our collections of *Hevea* from this and other regions are composed of much material originally planted by the Indians and from progeny of those planted trees, hybridized with the local jungle trees, which have sprung up in ancient and recent clearings.

Man along the Amazon has unconsciously and inconspicuously been changing the natural habitat of *Hevea* along the main waterways for centuries. He has made conditions under which interspecific hybridization within *Hevea* has been greatly facilitated and encouraged over large areas. He has aided in obscuring some distributional patterns along the rivers and certainly has contributed to many

perplexing cases of introgression (Seibert, '47). Through this he probably has done more than we realize to cause the extreme variability of *Hevea* found along the Río Negro. As far as I am able to learn from material seen, this variability reaches a very high degree in *Hevea pauciflora* (Spruce ex Benth.) Muell.-Arg. *H. pauciflora* appears as a major constituent in most of the hybrids and hybrid swarms along the upper Amazon proper and the Río Negro, evidently having hybridized with most of the other species of that region. This species is causing the most taxonomic discordance and it appears to have the greatest variation in seed size (Seibert, '47). It may be possible that *H. pauciflora* was the species which the Indians preferred as a nut tree and consequently attempted most often to domesticate. The rubber is very poor, and in hybrids originating from it as one parent, this characteristic seems to predominate. *H. pauciflora* is outstanding, however, in its resistence to the virulent South American Leaf Blight, *Dothidella Ulei* P. Henn. The Río Negro, though abundant in species and variations, is not known as a superior rubber-producing area, though it may prove to be highly significant as a region of outstanding disease-resistant strains.

Hevea has aided man in his advance in civilization. A study of its early history as a wild and cultivated nut tree is resulting in information useful in the task of improving commercial planting material of the *Hevea* rubbertree. It is not too optimistic to prophesy that modifications of its original jungle use may again be taken up as by-products of commercial plantings. Further experimental work is needed to test the qualities of these by-products. The seed kernels contain a high percentage of oil which is chiefly used in soap, but, being quick-drying, would also be of value in the paint industry. Stock feed and fertilizer may be manufactured from the remaining seed pulp (Jamieson, '43).

SUMMARY

1. Through its value as a food plant to the Indians of the Río Negro region, it appears that *Hevea* became a semi-domesticated tree.

2. Its domestication along the major waterways in clearings, edges of villages, and camp-sites followed a pattern of conscious or unconscious selection for seed production.

3. The planting of certain species in the vicinity of other wild species substantially aided the process of interspecific hybridization.

4. The spot-clearing and shifting type of agriculture practiced along the rivers for centuries resulted in types of habitats ideal for the growth and development of interspecific hybrids and hybrid swarms.

5. Once established in clearings the mature hybrids and introgressive hybrids are (at least in part) capable of competing with the encroaching second growth.

6. Several centuries of this slow process seem to have played a conspicuous part in the resultant hodge-podge of variables turning up as representative collections of *Hevea* from the Río Negro.

7. The "Peach-palm, *Guilielma Gasipaes*, may prove to be a classic example of the extent to which a tree has become domesticated in the Amazon valley, passing from Indian tribe to Indian tribe, from region to region, eventually reaching the West Indies and Central America.

8. From present evidence it appears that *Hevea pauciflora* has been the species of *Hevea* most cultivated by the Indians of the Río Negro and upper Amazon.

9. The Río Negro region is not outstanding as a region of high rubber yield or quality.

10. The past history of semi-domestication of *Hevea* in the Río Negro region may be significant in having strengthened disease resistance within certain species of that region.

11. The seeds of *Hevea* are a potential source of economic products useful to man.

12. Many of our cultivated plants probably had similarly complex histories.

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THE USE OF GLANDS IN A TAXONOMIC CONSIDERATION OF THE FAMILY BIGNONIACEAE[1]

R. J. SEIBERT[2]

Some genera of the family Bignoniaceae are important in the lumber industry of tropical regions, and many others hold unlimited horticultural possibilities. From a practical standpoint, therefore, horticulturists, foresters, and systematists need means of recognizing this multitude of conspicuous tropical plants. The use of floral characters in generic delimitation has been inadequate. Fruit characters have been satisfactory but it is only rarely that fruiting specimens are collected, and many species have been dubiously placed generically because the fruit has been incompletely studied or not observed. Too little attention has been given to vegetative characters in a taxonomic consideration of the Bignoniaceae.

Many bignoniaceous representatives are deciduous or flower before the appearance of leaves. Particularly in the lianas, the leaves vary with the part of the plant from which they are growing. More often than not, leaf specimens collected from the top of the plant, climbing through the trees, may be small and delicate while those near the base of the same plant are apt to be large, leathery, and of a different shape. It frequently is difficult to realize that the same species, in fact the same plant, could produce such unlike leaves.

As early as 1864, Bureau[3] recognized and discussed various types of glands in the family, but made no use of them in any practical way. K. Schumann[4] made some beginnings in the taxonomic utilization of the glands, but it was Sandwith[5] who first successfully used them as key characters and as significant features in specific descriptions. His ideas have been critically examined and found to be most practical in application.[6]

More types of glands are found in the lianas in general than in the tree members of the family. The tribe Bignonieae, representing most of the lianas, may be divided into two groups on the basis of glands alone. One group has them located at the nodes between the petioles while the other group has no evidence of glandular regions at the nodes but, rather, has more or less distinct ridges between the petioles. Both functional and apparently non-functional glands are found. In some instances the secretions are quite odoriferous. Occasionally secretions from the glands, particularly those in the axils of the lateral leaflet veins and on the

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[1] This paper was prepared in connection with studies carried on while the writer was a graduate student at the Missouri Botanical Garden.

[2] Agent (Botanist) Division of Rubber Plant Investigations, Bureau of Plant Industry, Soils and Agricultural Engineering, Agricultural Research Administration, United States Department of Agriculture.

[3] Bureau, Edouard. Monographie des Bignoniaceae. pp. 164–169. Paris, 1864.

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[5] Sandwith, N. Y. Bignoniaceae—Flora of Surinam 4^{2}:1–86. Edited by A. Pulle. 1938.

[6] Seibert, R. J. The Bignoniaceae of the Maya area. Carnegie Inst. Washington, Publ. 522:375–434. 1940.

calyx, have been found to permit growth of specialized fungi. It seems safe to say that glands, as represented in the family Bignoniaceae, may be utilized to advantage in a taxonomic treatment. Certain types of glands fit in harmoniously with the present system of classification based on the fruit. In combination with other characters they prove useful in generic as well as in specific delimitation, greatly facilitating identification in sterile material.

TYPES OF GLANDS REPRESENTED IN THE FAMILY BIGNONIACEAE

INTERPETIOLAR GLANDS:

Fields of rather closely crowded glands may be found on either side of the stem, at the nodes between the petiole bases, rarely slightly above them (pl. 3, figs. 1–3). The glands are somewhat saucer-shaped and depressed in the stem tissue, giving a pitted appearance usually discernible to the naked eye. They are multicellular structures attached to the epidermis by a single very large cell (pl. 6, fig. 1). Apparently this attachment cell had its origin as an epidermal cell which became much enlarged and pushed up from the epidermis proper.

The size and number of interpetiolar glands in the fields vary considerably, depending on the genus. Interspecific variation within some genera is sufficiently constant to be of material taxonomic aid. These fields are usually most apparent on young branchlets, and frequently are completely obliterated in the second or third year. However, in such genera as *Ceratophytum* and *Pachyptera* they may become more conspicuous in the older plants, in which case the tissue grows partially around them, producing deep pits or depressions.

Interpetiolar glands form a basis for dividing the lianas into two subdivisions. With very few exceptions each species within a particular genus has a rather characteristic field as regards size, shape, and number and size of the glands. Only in the genus *Neomacfadya* are these glands difficult to see, and there one is often compelled to search several nodes with the aid of a lens.

The following representative genera are characterized by having interpetiolar glands:

Arrabidaea	*Macfadyena*	*Potamoganos*	*Scobinaria*
Ceratophytum	*Neomacfadya*	*Pseudocalymma*	*Tanaecium*
Lundia	*Pachyptera*	*Saldanhaea*	

NEURO-AXILLARY GLANDS:

Glandular structures may be located in the axils of the lateral veins, on the lower surface of the leaves or leaflets. In structure and diversity they are quite similar to those found on the leaves within the Apocynaceae and Lauraceae. In the Bignoniaceae they are not characteristic of all species within a particular genus, and hence they frequently may be used to advantage in specific delimitation.

Two distinct types of neuro-axillary glands are represented with considerable variation within each type. In a few instances some border-line conditions have been noted grading more or less into each other.

Domatia or *Coeliac Glands.*—These are modified cavities in the axils of the lateral veins (pl. 4, figs. 1, 2). They frequently furnish shelters for scale and other small insects. Depending on the species, they run the gamut from a tufted-pubescent axil to a very deep cavity with a ciliated orifice. Their structure is quite constant within the species and usually they are easily seen with the naked eye. In such few cases as characterized by *Arrabidaea obliqua* the cavity may be much in evidence on the upper surface of the leaflet as a dome-shaped protuberance (pl. 4, fig. 3).

Glandular Fields.—Areas of closely crowded glands are sometimes immersed in the tissue (pl. 4, figs. 4, 5). Morphologically they are similar to the interpetiolar glandular fields (pl. 7, fig. 1), and frequently they are secretory structures. The secretions may be odoriferous, as in *Anemopaegma Chamberlaynii,* where a skunk-like odor is emitted, or as the "bejuco de ajo" (*Pseudocalymma* sp.) which emits a strong garlic odor. It is to be noted that a fungus was found growing in the odoriferous secretion of the glands of *Anemopaegma Chamberlaynii.*

Representative species characterized by having neuro-axillary domatia or glandular fields are:

Amphilophium paniculatum (L.) HBK.
Anemopaegma Chamberlaynii (Sims) Bur. & K. Schum.
Arrabidaea candicans (L. C. Rich.) DC.
Arrabidaea floribunda (HBK.) Loes.
Arrabidaea obliqua (HBK.) Bur.
Catalpa (all species)
Ceratophytum tobagense (Urb.) Sprague & Sandw.
Chodanthus puberulus Seibert
Cydista aequinoctialis (L.) Miers
Cydista diversifolia (HBK.) Miers
Cydista heterophylla Seibert
Cydista pubescens Blake
Onohualcoa fissa (Loes.) Sandw.
Parmentiera (all species)
Pseudocalymma laevigatum (Bur. & K. Schum.) Semp. & Kuhlm.
Pseudocalymma macrocarpum (Donn. Sm.) Sandw.
Pyrostegia venusta (Ker) Miers
Spathodea campanulata Beauv.
Tabebuia pentaphylla (L.) Hemsl.
Tecoma stans (L.) HBK.
Tynanthus guatemalensis Donn. Sm.

PETIOLAR GLANDS:

A field of conspicuous glands may be found at the terminal end of the petioles below their junction with the petiolules (pl. 3, figs. 4, 5). They are the rarest type of gland found in the family and, being represented only in *Pachyptera* and *Pseudocalymma,* they serve as an excellent means of recognizing these two genera when only sterile material is at hand. It is to be noted that both these genera are also characterized by very prominent interpetiolar glands.

CALYX GLANDS:

Submerged or somewhat impressed functional glands are usually located on the upper half of the calyx tube or on the lobes (pl. 5, fig. 1), usually arranged in rows. They are quite conspicuous in living material and exude large globules of colorless, viscous liquid. In structure they generally are like those found in the axils of the lateral leaflet veins or on the stems between the petioles, that is, multicellular saucer-shaped glands attached by a single very large cell. However, in the large, inflated calyces of *Callichlamys latifolia* the glands are exceptionally large, completely submerged, and attached by a considerable number of rather

large cells, in no way as conspicuous as the single large attachment cell of the other types (pl. 7, fig. 2).

Microtome sections made through the calyx glands of *Callichylamys latifolia* showed them to be infected by a member of the Melanconiales. The fungus appears to grow well in the material exuded, and hyphae have been traced down through the gland into the attachment cells. Nothing more than the gland itself was seen to have been infected.

The following genera may be said to be characterized by conspicuous glands on the calyx:

Adenocalymma	*Crescentia*	*Memora*	*Scobinaria*
Anemopaegma	*Cydista*	*Pachyptera*	*Tanaecium*
Astianthus	*Distictella*	*Pleonotoma*	*Tecoma*
Callichlamys	*Enallagma*	*Paragonia*	
Campsis	*Martinella*	*Pithecoctenium*	
Ceratophytum	*Macfadyena*	*Roentgenia*	

COROLLA GLANDS:

Partly immersed saucer-shaped glands are sometimes found in rows near the base of the corolla lobes (pl. 5, fig. 2). They may be either on both sides or at the center of the lobe base, and may extend a short distance down the throat. When present, they are very conspicuous but are found only in a few genera, as characterized by *Pachyptera, Pleonotoma* and *Memora.* In *Adenocalymma* corolla glands are confined only to a few of the species, best exemplified by *A. inundatum* Mart.

PSEUDOSTIPULAR GLANDS:

Partly immersed glands on the pseudostipules may be found on nearly all species in which pseudostipules appear. The glands are dispersed with no definite arrangement in rows or fields. Taxonomically they appear to be of little use.

PELLUCID GLANDS:

These glands, located on the leaflets, are quite similar to the familiar pellucid glands on the leaves of the Rutaceae. They are yellowish orange when viewed under a lens. By holding the specimen to the light they may be seen as numerous, small but conspicuous, translucent spots. Only four genera are characterized by having pellucid glands: *Amphilophium, Pithecoctenium, Pyrostegia,* and *Stizophyllum.*

SCATTERED GLANDS:

Scattered impressed saucer-shaped glands are mostly found on the surface of the leaflets. There is no definite arrangement except that they are usually close to the main veins (pl. 4, fig. 3). They frequently are a constant character within a species.

GLANDULAR SCALES:

Minute scales may be found on stems, petioles, leaves, calyx, corolla, ovary and fruit, and are responsible for the "lepidote" condition so frequently encountered in the Bignoniaceae. So far as is known, they never are secretory. The glandular (lepidote) scales are multicellular structures attached to a slightly modified

epidermal cell or cells (pl. 6, figs. 2, 3). They may be subdivided into three types as follows:

Sessile.—Somewhat immersed or resting on the surface of the tissue and attached to an epidermal cell.

Stipitate.—Attached to the epidermis by a short, few-celled stalk. This type is rare, being most conspicuously represented in the genus *Mussatia,* where they are found on the outer corolla surface.

Punctate.—In maturity, natural removal of somewhat immersed sessile glandular scales leaves a punctate condition found on leaflet surfaces of a number of species.

Glandular scales are most conspicuous on leaflets (pl. 4, fig. 4; pl. 6, fig. 3), ovaries (pl. 6, fig. 2), calyces, and especially corollas. When seen on the outer surface of the corolla one may expect to find that every species of that genus will have lepidote corollas. The following genera are characterized by glandular (lepidote) corollas:

Anemopaegma	*Crescentia*	*Martinella*	*Pleonotoma*	*Stizophyllum*
Callichlamys	*Cydista*	*Mussatia*	*Pseudocalymma*	*Tecoma*
Clytostoma	*Enallagma*	*Neomacfadya*	*Roentgenia*	

CAPITATE GLANDULAR HAIRS:

Hairs having multicellular capitate glands at the apex may be located on stems, petioles, leaflet veins, calyces, and staminodia (pl. 7, figs. 3, 4, 5). In *Jacaranda* they are always located on the staminodia, and by the relative length, density, distribution, and placement of these hairs on the staminodia it is possible to distinguish many of the species of this genus. Usually they are most densely disposed in the region nearest the anthers where they may serve as nectaries to aid in insect pollination.

Other than in *Jacaranda,* few genera have capitate glandular hairs, and then only on isolated species. *Arrabidaea mollissima* (HBK.) Bur. & K. Schum. may be cited as characteristically having them on the young branchlets, petioles, and inflorescence branches, where they are scattered throughout the other shorter, normal pubescence.

Explanation of Plate

PLATE 4

NEURO-AXILLARY GLANDS

Fig. 1. Portion of the lower leaflet surface of *Ceratophytum tobagense* (Urb.) Sprague & Sandw., showing a domatium or modified cavity in the axil of a lateral nerve.

Fig. 2. Domatia in the axils of the lateral nerves on the lower surface of a leaflet of *Arrabidaea obliqua* (HBK.) Bur.; × ¾.

Fig. 3. Evidence of domatia as seen on the upper surface of a leaflet of *Arrabidaea obliqua*. Scattered glands may be observed in close proximity to the mid-vein; × ¾.

Fig. 4. Glandular fields in the axils of the lateral veins on the lower leaflet surface of *Anemopaegma Chamberlaynii* (Sims) Bur. & K. Schum. The glandular scaly or lepidote condition of the lower surface may be clearly seen.

Fig. 5. Portion of the lower leaflet surface of *Cydista heterophylla* Seib. showing glandular fields in the axils of the main lateral veins.

Explanation of Plate

PLATE 3

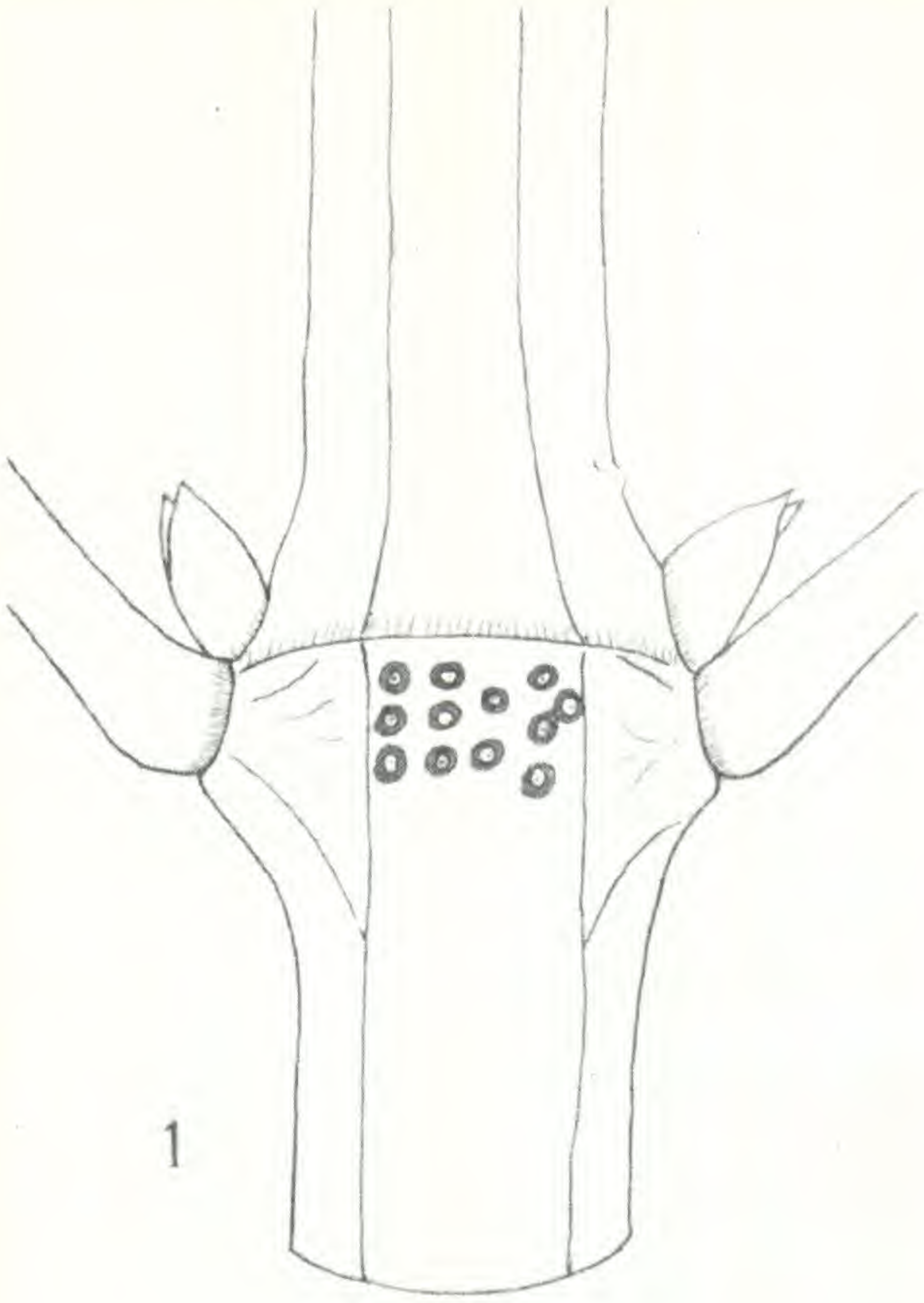
Fig. 1. Interpetiolar glands at the node of *Pseudocalymma* sp.

Fig. 2. Interpetiolar glands at the node of *Arrabidaea Blanchetii* DC.

Fig. 3. Interpetiolar glands at the terminal node of a young branch of *Pachyptera Kerere* (Aubl. emend Splitg.) Sandw.

Fig. 4. Petiolar glands of *Pachyptera Kerere* showing their position at the terminus of the petiole below the junction of the petiolules.

Fig. 5. Petiolar glands of *Pachyptera Kerere*.



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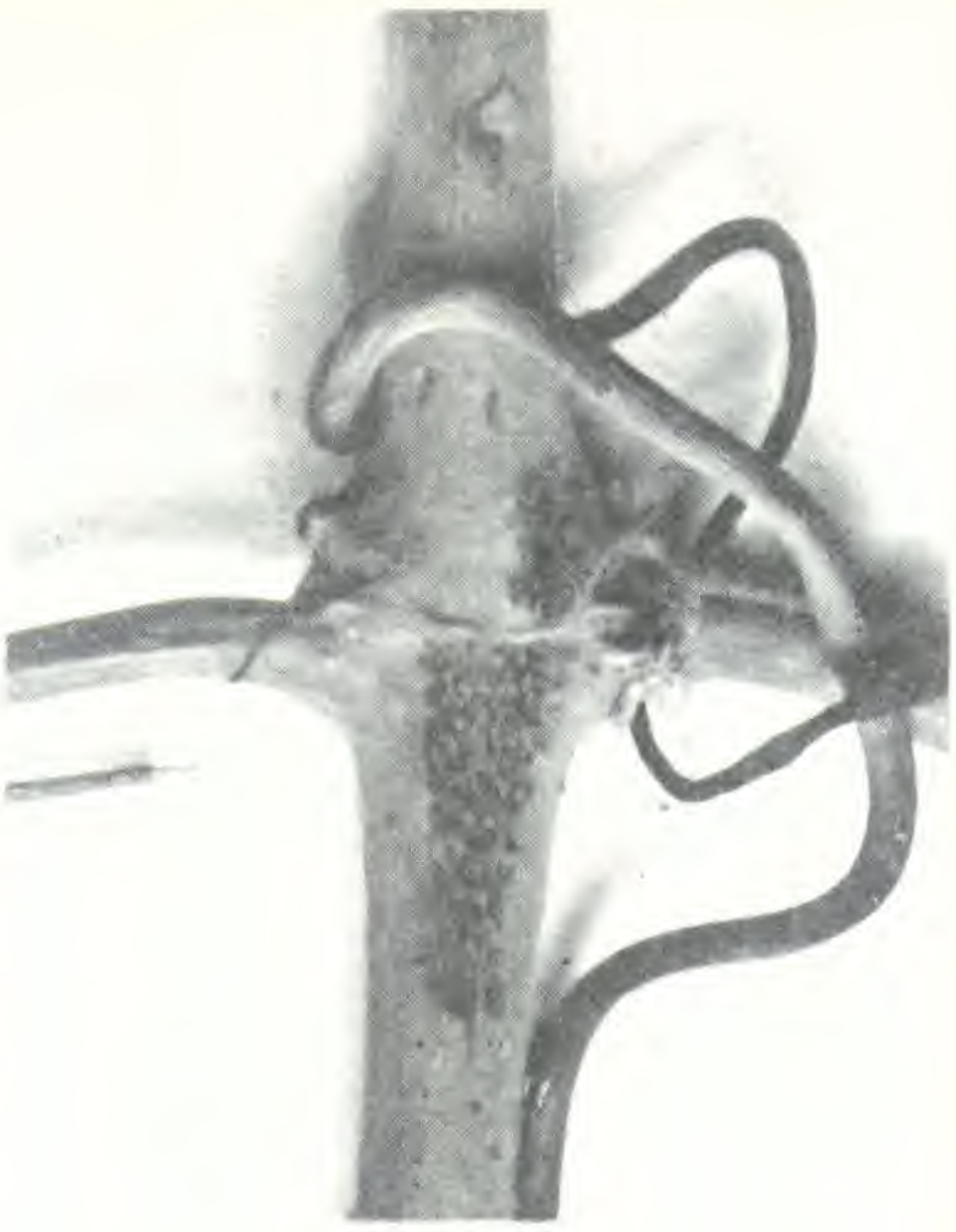

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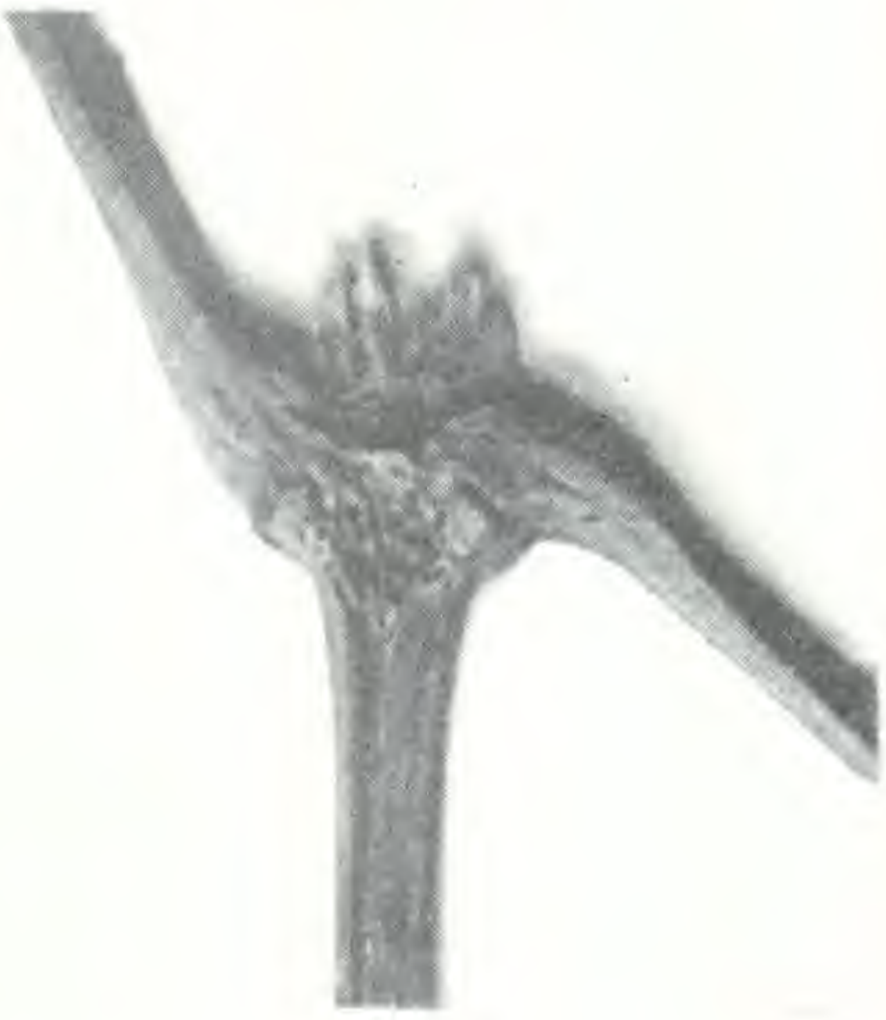

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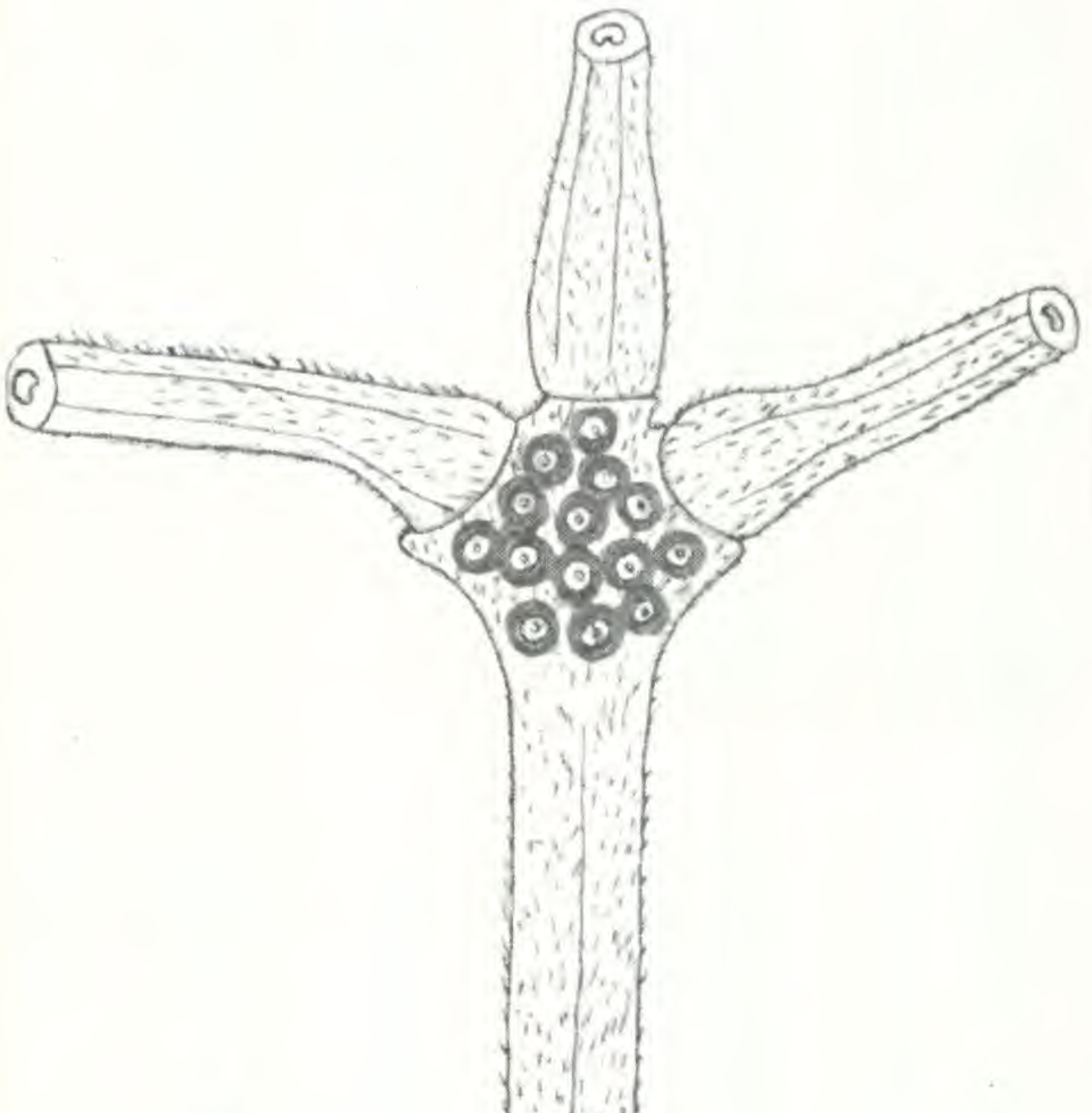

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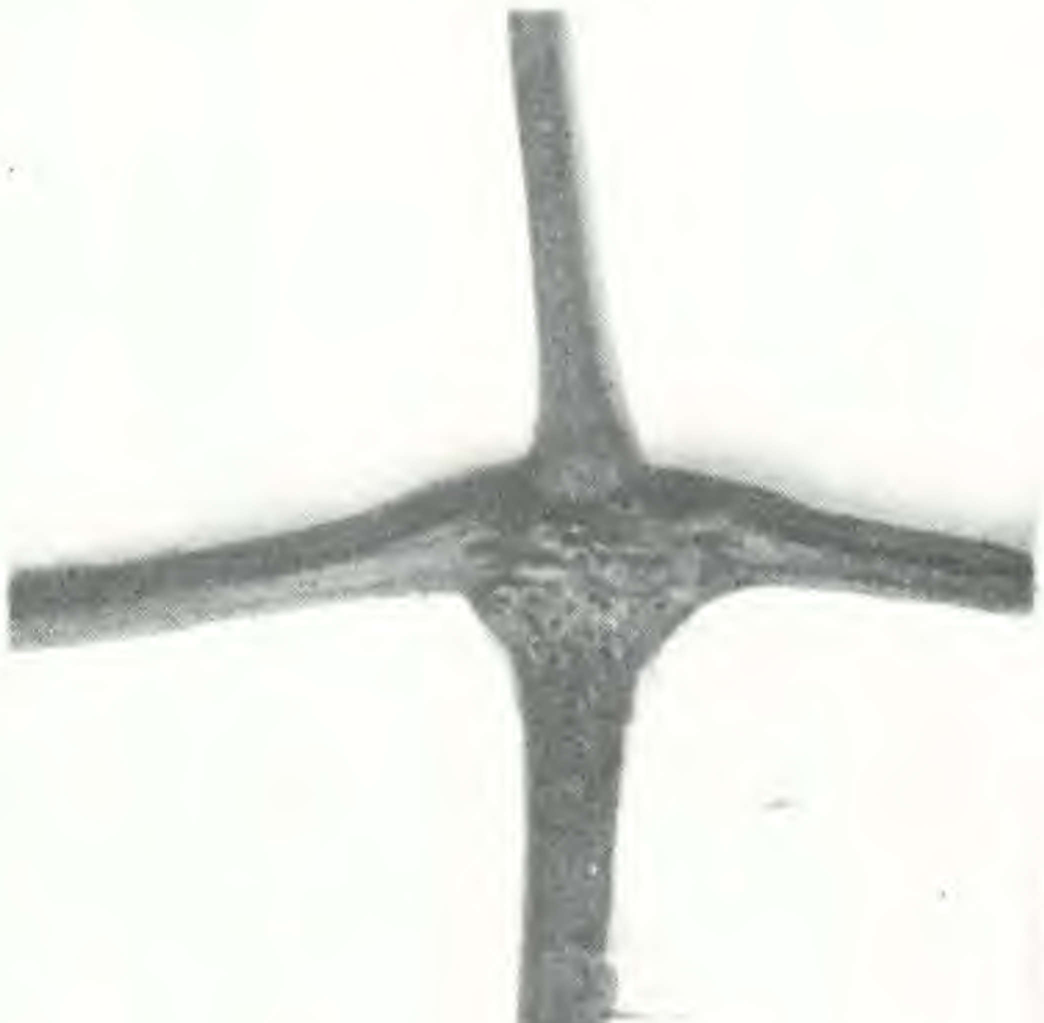


5

SEIBERT—GLANDS IN THE BIGNONIACEAE

Explanation of Plate

PLATE 4

NEURO-AXILLARY GLANDS

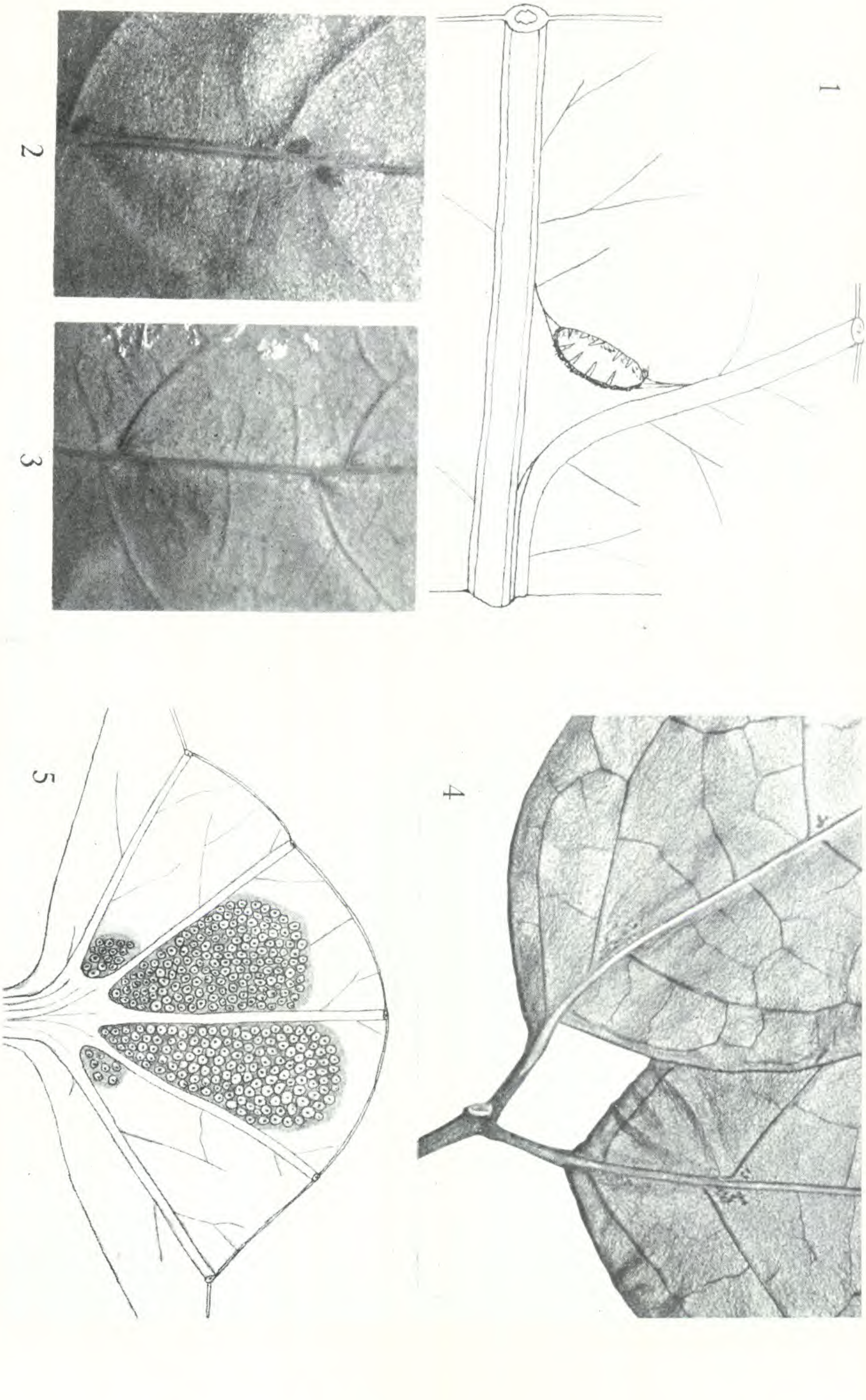
Fig. 1. Portion of the lower leaflet surface of *Ceratophytum tobagense* (Urb.) Sprague & Sandw., showing a domatium or modified cavity in the axil of a lateral nerve.

Fig. 2. Domatia in the axils of the lateral nerves on the lower surface of a leaflet of *Arrabidaea obliqua* (HBK.) Bur.; × ¾.

Fig. 3. Evidence of domatia as seen on the upper surface of a leaflet of *Arrabidaea obliqua*. Scattered glands may be observed in close proximity to the mid-vein; × ¾.

Fig. 4. Glandular fields in the axils of the lateral veins on the lower leaflet surface of *Anemopaegma Chamberlaynii* (Sims) Bur. & K. Schum. The glandular scaly or lepidote condition of the lower surface may be clearly seen.

Fig. 5. Portion of the lower leaflet surface of *Cydista heterophylla* Seib. showing glandular fields in the axils of the main lateral veins.



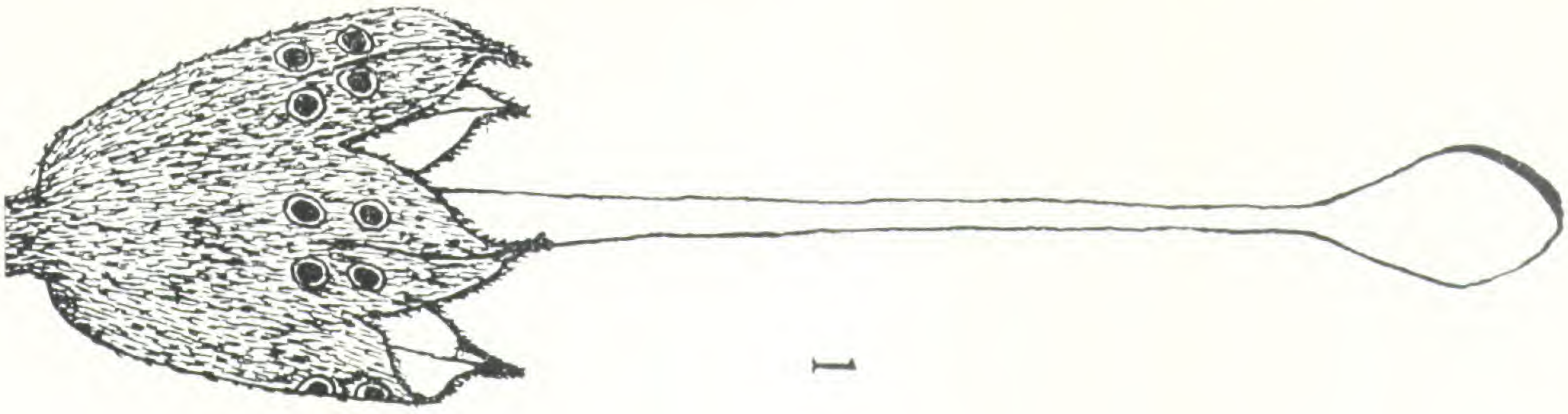
SEIBERT—GLANDS IN THE BIGNONIACEAE

Explanation of Plate

PLATE 5

Fig. 1. Position of the glands on the calyx of *Adenocalymma bracteatum* (Cham.) DC.; × 4.

Fig. 2. Corolla glands at the base of the lobes of *Memora Klugii* Standl.; × 4.



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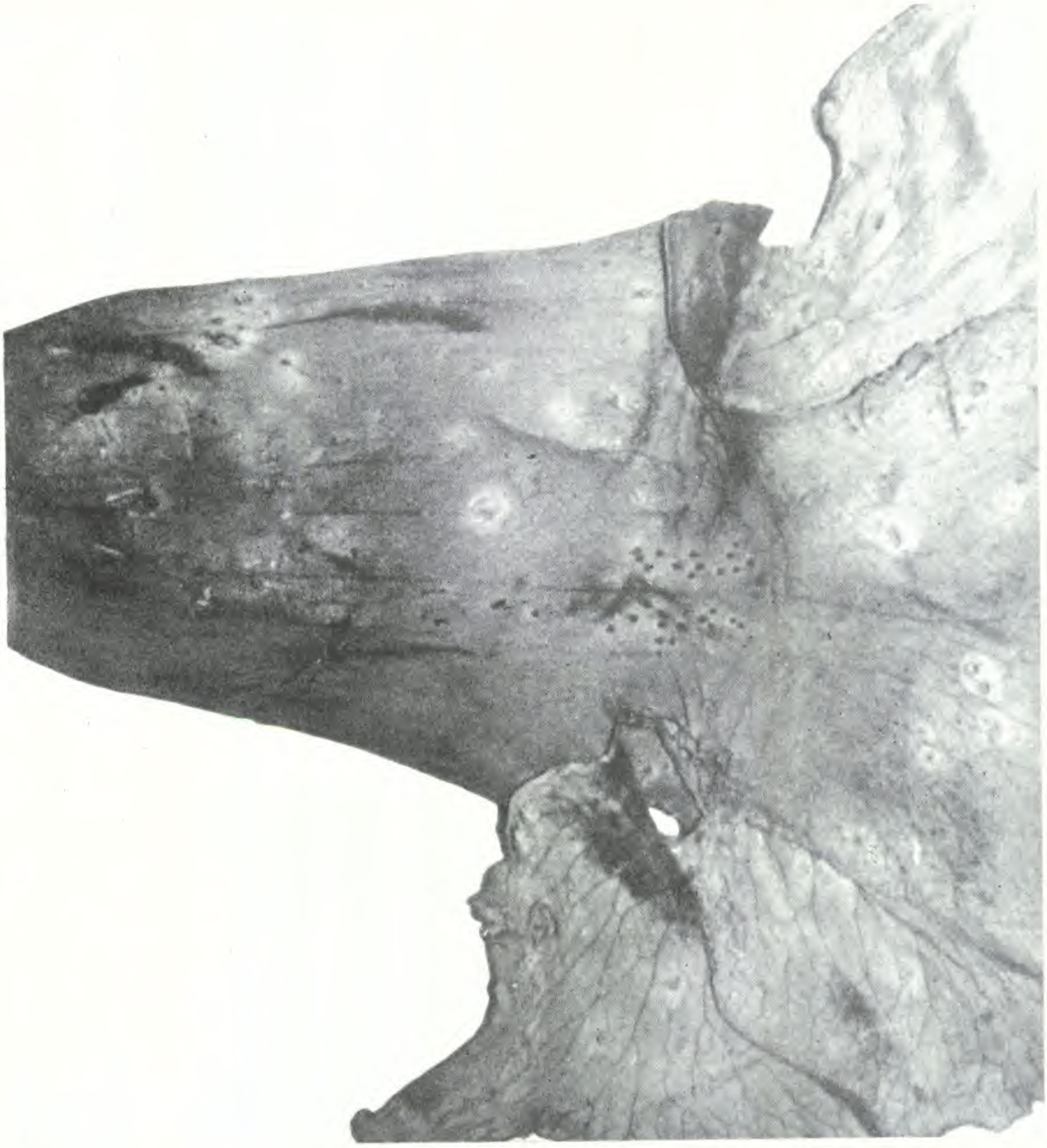


2

SEIBERT—GLANDS IN THE BIGNONIACEAE

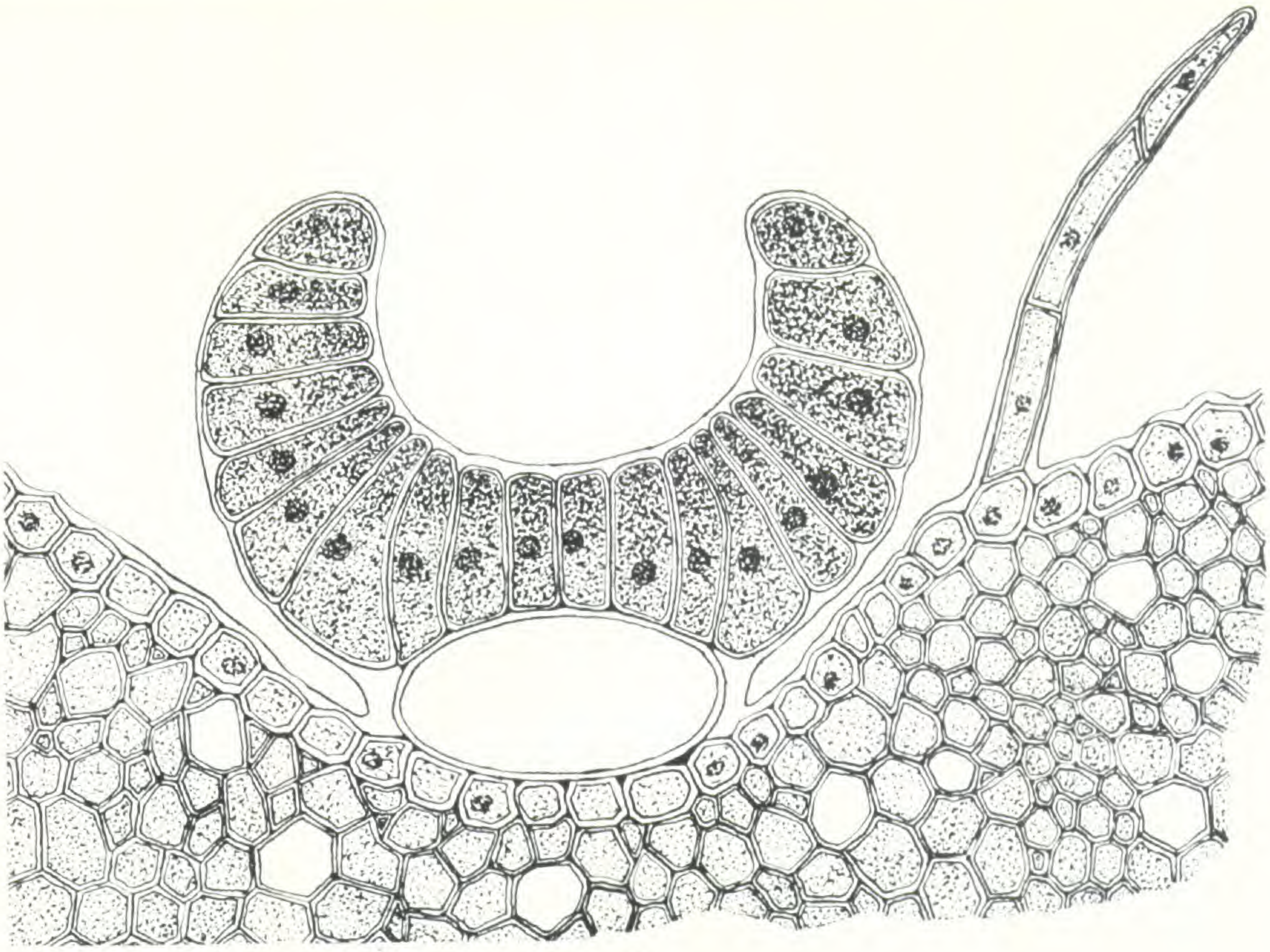
Explanation of Plate

PLATE 6

Fig. 1. *Lundia corymbifera* (Vahl) Sandw. Cross-section through the node on a young stem showing detail of an interpetiolar gland.

Fig. 2. *Anemopaegma Chamberlaynii* (Sims) Bur. & K. Schum. Section through the ovary showing detail of the glandular scales on the outer surface.

Fig. 3. Section through the lower leaflet surface of *Anemopaegma Chamberlaynii*, showing detail of a somewhat immersed glandular scale.



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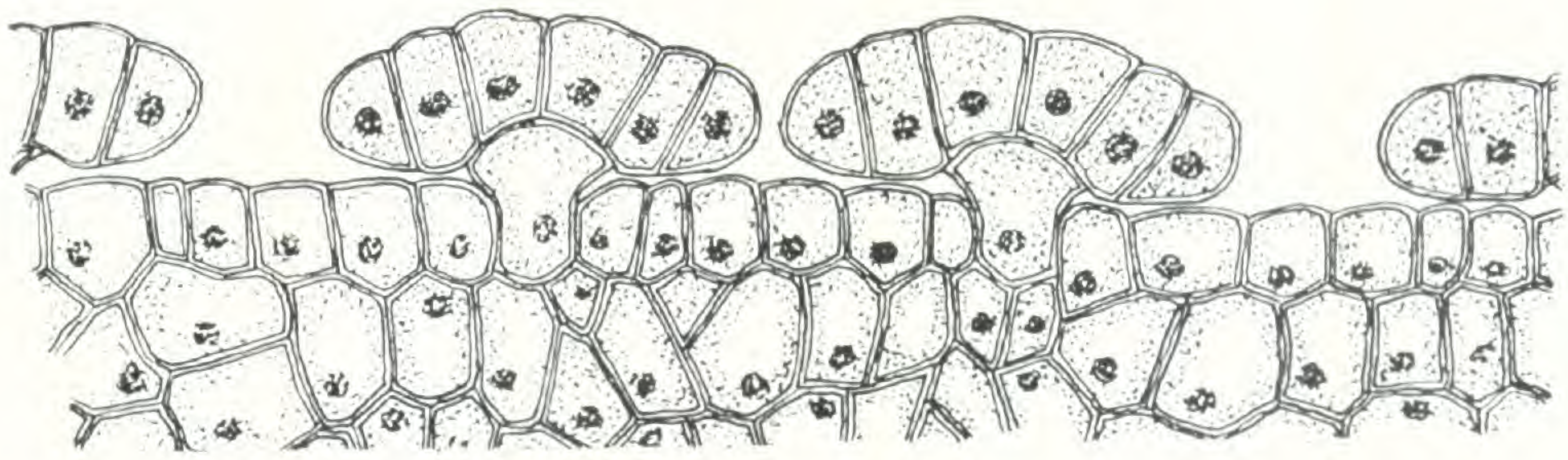

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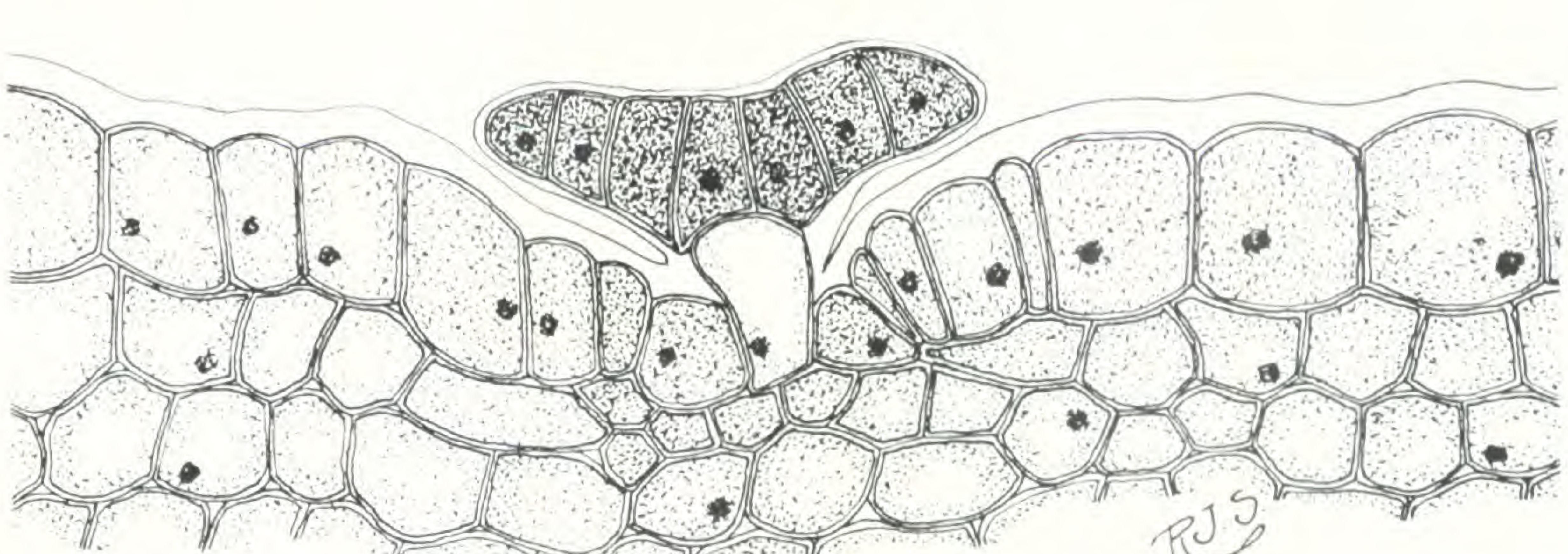


3

SEIBERT—GLANDS IN THE BIGNONIACEAE

Explanation of Plate

PLATE 7

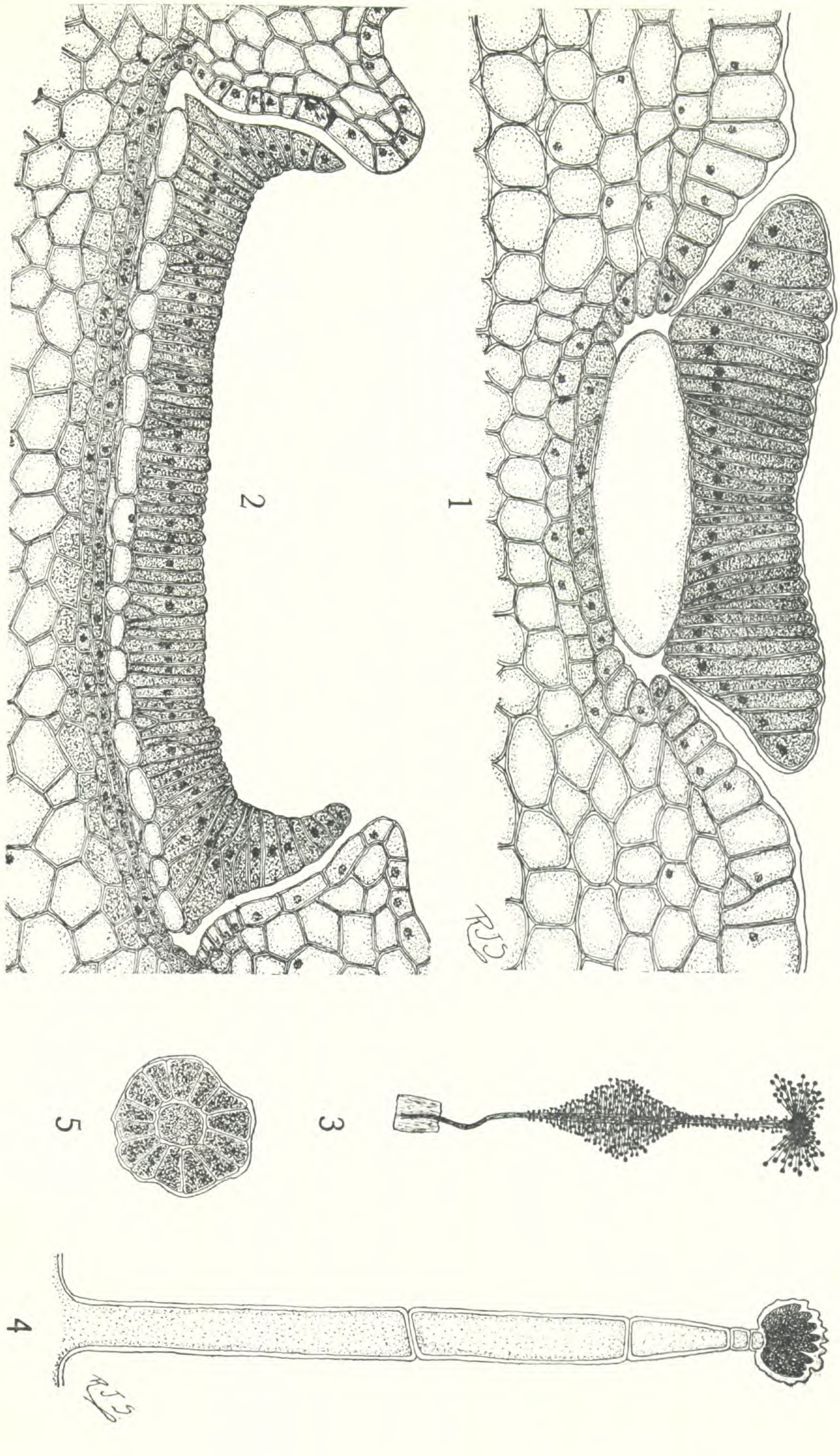
Fig. 1. *Anemopaegma Chamberlaynii* (Sims) Bur. & K. Schum. Section through a glandular field in the axil of a lateral leaflet vein showing detail of one of the glands.

Fig. 2. *Callichlamys latifolia* (L. C. Rich.) K. Schum. Section through the inflated calyx showing detail of a large immersed gland.

Fig. 3. *Jacaranda mimosifolia* D. Don. Staminodium showing relative size, density, distribution, and length of the capitate glandular hairs; × 3.

Fig. 4. Detail of a capitate glandular hair from the staminodium of *Jacaranda mimosifolia;* × 30.

Fig. 5. Looking down on the upper surface of a capitate glandular hair from the staminodium of *Jacaranda mimosifolia;* × 25.



SEIBERT—GLANDS IN THE BIGNONIACEAE

GYNANDROPSIS, CLEOME, AND PODANDROGYNE

ROBERT E. WOODSON, JR.

The genus *Gynandropsis* was established by de Candolle[1] in 1824 and supplied with nine species indigenous to the tropics and subtropics of both hemispheres, largely segregates from the Linnaean *Cleome.* The separation of the two genera was based upon the "torus": that of the latter "*subhemisphaericus,*" and that of the former "*elongatus.*" The separation was accepted generally and promptly, although with various phrasing by different authors ("Androphor kurz oder fehlend" *vs.* "Androphor entwickelt, deutlich"—Pax & Hoffman; "Stamens free" *vs.* "Stamens attached to the gynophore"—Fawcett & Rendle).

The flowers of *Cleome* and of *Gynandropsis,* as originally segregated, normally are hermaphrodite; hence the publication by Bentham[2] in 1845 of two monoecious species from the northern Andes, *G. coccinea* and *G. densiflora,* was of particular interest. Bentham described the inflorescences of his species as bearing staminate flowers toward the tip and pistillate flowers toward the base. Not until later was it appreciated that two of de Candolle's original species also possessed this character, namely *G. brachycarpa* and *G. hispidula,* also of the northern Andes.

In 1854, Turczaninov[3], apparently unaware of Bentham's publication, proposed several additional South American species of *Gynandropsis,* some of them synonymous with those of the earlier author. This article is particularly interesting, however, in the implied (but unfortunately not formally proposed) segregation of the hermaphrodite species into the section *Eugynandropsis,* and those with monoecious flowers into the sections *Hymenadenia* and *Gyradenia.* Although recognizing *Gynandropsis* merely as a section of *Cleome,* Triana & Planchon[4] also divided the Colombian species into two unnamed subsections having the flowers hermaphrodite or monoecious, respectively. Also noteworthy in this latter treatment is the description of *Cleome (Gynandropsis) decipiens,* a peculiar plant bearing large, simple leaves in contrast to the palmately compound leaves of other species of *Gynandropsis.* The discernment of these three early authors puts to shame their successors who ignored them for over three-quarters of a century.

In 1891, Pax[5] discarded *Gynandropsis* in favor of the earlier *Pedicellaria* Schrank[6], but in 1930 the former name was conserved by the Cambridge Congress[7], and the lectotype proposed as *G. pentaphylla* (L.) DC., a hermaphrodite species.

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[1] DC. Prodr. 1:237. 1824.
[2] Benth. Pl. Hartw. 160. 1845.
[3] Turcz. in Bull. Soc. Nat. Moscou 27^2:313. 1854.
[4] Tr. & Pl. Prodr. Fl. Novo Gran. 70. 1862.
[5] Pax, in Engl. & Prantl, Nat. Pflanzenfam. ed. 1. 3^2:223. 1891.
[6] Schrank, in Roemer & Usteri, Mag. 3:10. 1790.
[7] Int. Rules, ed. 3. 97. 1935.

Issued June 22, 1948.

In 1930, Ducke[8] published the genus *Podandrogyne* from eastern Peru. Ducke appreciated the relationship of his genus to the monoecious species of *Gynandropsis* but, paradoxically, was handicapped, on the one hand, by the excellence of his study collection and, on the other, by ignorance of the fruiting habit of the species of monoecious *Gynandropsis*. Hence, the primary characters of his *Podandrogyne* were fruiting characters: "*Cleomoideis . . . differt replo nullo valvis post dehiscentiam irregulariter contortis.*" Ducke's illustration of *P. glabra*, the monotype, is excellent in detail of the simple-leaved (cf. *Cleome decipiens* Tr. & Pl.) species with monoecious flowers in an ebracteate raceme, with the peculiarly contorted replum (sic!) of the irregularly dehiscent silique. Also drawn with careful detail is a character apparently unappreciated by the author: the conspicuous membranaceous, funicular aril of the seed!

During the preparation of my account of Capparidaceae for the 'Flora of Panama,' compiled by Dr. Schery and myself[9], I have had the opportunity to examine numerous specimens of *Gynandropsis* from South America as well as from Panama, and have found it easy to demonstrate that all monoecious species of *Gynandropsis*, whether bearing simple or palmately compound leaves, produce fruit with the peculiar silique dehiscence and arillate seeds so well illustrated by Dr. Ducke. The fruit, however, is not actually without a replum, as may easily be observed from any specimen. But, except possibly in the case of *G. brachycarpa* DC., the pericarp appears to rupture irregularly without the customary abscission of the two valves, and the replum abjuncts at the apex, later undergoing the characteristic contortion. These features surely must have been displayed by the rich South American collections at Berlin, and it is difficult to understand how Pax & Hoffman[10] could see fit to erect a new subfamily, Podandrogynoideae, for the monotypic *Podandrogyne*, while leaving the numerous monoecious species within *Gynandropsis* of the Cleomoideae.

The Capparidaceae are a fascinating family which has not been studied effectively in its American representation since 1865[11]. Were I to undertake such a study, I am sure that I should return the hermaphrodite species of *Gynandropsis* to *Cleome*, since it would be an easy task to reveal the unreliable nature of the "torus" character, unsupported as it is by any other. The problem is one of considerable magnitude, however, and one which I must leave to another. Nevertheless, I do feel competent at the present time to append to this discussion a brief synopsis emending the genus *Podandrogyne* to include all monoecious species of *Gynandropsis*.

My study collection consists chiefly of specimens deposited in the herbaria of the Missouri Botanical Garden and the Chicago Natural History Museum, augmented by certain material from the U. S. National Herbarium and the Royal

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[8]Ducke, in Archiv. Jard. Bot. Rio Jan. 5:115. *pl. 7.* 1930.
[9]Woodson & Schery, in Ann. Missouri Bot. Gard. 35:75. 1948.
[10]Pax & Hoffm. in Engl. & Prantl, Nat. Pflanzenfam. ed. 2. 17b:208. 1936.
[11]Eichl. in Mart. Fl. Bras. 13^1:238. 1865.

Botanic Gardens, Kew. Types from continental European herbaria are represented by photographs prepared by J. Francis Macbride through the Rockefeller Fund.

PODANDROGYNE Ducke, emend.

PODANDROGYNE Ducke, in Archiv. Jard. Bot. Rio Jan. 5:115. 1930.

Gynandropsis DC. Prodr. 1:237. 1824, in part.

Erect or ascending, suffrutescent or suffruticose herbs; leaves alternate, simple or palmately compound, exstipulate; inflorescence racemose or corymbose, terminal, several- to many-flowered, bracteate or ebracteate; flowers monoecious, rarely andromonoecious or dioecious through abortion, the lower flowers pistillate, the upper staminate; calyx more or less deeply 4-parted, persistent or deciduous, sometimes more or less petalaceous; petals 4, more or less unequal, usually unguiculate; disc usually manifest, symmetrical or eccentric; fertile stamens 6, inserted on a short or moderately elongate, concentric or eccentric gynophore, the filaments somewhat unequal and declinate, the anthers dorsifixed near the base, accompanied by an abortive pistillode; fertile ovary borne upon a manifest, concentric or eccentric gynophore, the stigma capitate, sessile or stipitate, the ovules numerous, the accompanying staminodia greatly reduced, sagittate, borne upon a manifest androgynophore; fruit a dry, terete or somewhat compressed silique, usually dehiscing irregularly, the replum finally separating at the tip (except in *P. brachycarpa*?) and irregularly contorted; seeds cochleate-reniform, with a conspicuous lamellate, funicular aril.

Type species: PODANDROGYNE GLABRA Ducke, loc. cit. 1930.

a. Androgynophores included, concentric, the disc inconspicuous and essentially radial, not enlarged and conspicuous in fruit.
  b. Leaves palmately compound, usually 3- to 7-foliolate; calyx lobes cleft nearly to the receptacle; Costa Rica and Panama (to Peru?).... 1. *P. chiriquensis*
  bb. Leaves simple; calyx campanulate, the lobes cleft about half or less to the receptacle; Colombia.... 2. *P. decipiens*
aa. Androgynophores exserted, conspicuously eccentric through the unilateral development of a thick disc which is enlarged and conspicuous in fruit.
  b. Leaves palmately compound, usually 3- to 7-foliolate, or the uppermost or lowermost occasionally simple.
    c. Fruits linear-oblongoid, much longer than the androgynophore.
      d. Inflorescence corymbose, greatly contracted, not secund, erect; Colombia and Ecuador.... 3. *P. coccinea*
      dd. Inflorescence racemose, relatively elongate, secund, somewhat cernuous; Venezuela.... 4. *P. cernua*
    cc. Fruits broadly oblongoid to ovoid, about as long as the androgynophore or somewhat shorter.
      d. Plants densely pubescent; leaflets 5–9; lowermost flowers frequently perfect; inflorescence frequently with more or less persistent, foliaceous bracts; Colombia to Bolivia.... 5. *P. brachycarpa*
      dd. Plants essentially glabrous; leaflets 3, or the lowermost or uppermost sometimes simple; flowers apparently always monoecious; inflorescence ebracteate; Colombia and Ecuador.... 6. *P. gracilis*
  bb. Leaves simple.
    c. Inflorescence relatively elongate, secund, somewhat cernuous.
      d. Calyx lobes ovate to ovate-lanceolate, acuminate, pale green suffused with pink; fruits clavate-oblongoid, about as long as

the androgynophore or somewhat shorter; Colombia and Venezuela .... 7. *P. macrophylla*
dd. Calyx lobes ovate-subreniform, obtuse, deep purple; fruits linear-oblongoid, about twice as long as the androgynophore; Colombia .... 8. *P. polychroma*
cc. Inflorescence congested, not secund, erect; Colombia to Peru and adjacent Brazil .... 9. *P. glabra*

1. Podandrogyne chiriquensis (Standl.) Woodson, in Ann. Missouri Bot. Gard. 35:85. 1948.

Gynandropsis chiriquensis Standl. in Jour. Wash. Acad. 17:252. 1927.
Gynandropsis pulcherrima Standl. loc. cit. 253. 1927.

COSTA RICA: *Standley & Valerio 44560; Dodge & Thomas 5628; A. Smith H. 481; A. Smith P.C. 361; Skutch 3627.* PANAMA: *White & White 50; P. White 168; Seibert 138, 334; Woodson, Allen & Seibert 859; Woodson & Schery 539; Davidson 180; Allen 1650, 219, 2730, 4780, 4956; Hunter & Allen 552.*

Standley's primary distinction between *G. chiriquensis* and *G. pulcherrima* is based upon number of leaflets: five in the former and three in the latter. The Costa Rican specimens enumerated above all have three leaflets, and one may judge that the eleven additional Costa Rican specimens enumerated by Standley are constant to that number. Amongst the Panamanian specimens before me, three from the province of Chiriquí bear 3-foliolate leaves, and seven bear leaves which are 5- to 7-foliolate. Farther east, in the province of Coclé, three plants again bear 3-foliolate leaves. Since I have been able to discover no additional character to separate *G. chiriquensis* and *G. pulcherrima,* I am unwilling to maintain the two species separately, although they might be regarded as varieties with rather poor geographical differentiation.

Whether *P. chiriquensis* extends into northern South America is a subject for conjecture because of our meagre representation of the genus. Two specimens before me, however, will fall to that species in the key which I have prepared, although they differ from the Central American population in certain respects; both are 3-foliolate: *Pennell 14073*, from the department of Cusco, Peru, is the type specimen of *Gynandropsis Herrerae* Macbr. (in Field Mus. Publ. Bot. 4:168. 1929); at first glance strongly recalling Costa Rican *G. pulcherrima,* this plant differs in the slightly more coherent calyx lobes, thus recalling *Podandrogyne coccinea. Cuatrecasas 11497*, from Comisaría del Putumayo, Colombia, also will key to *P. chiriquensis*, the calyx being rather typical of the latter species, but the mature fruits are scarcely half as long. It may well be that these two sheets represent two distinct species, but I am inclined to consider hybridization of *P. chiriquensis* with such typically South American species as *P. coccinea* and *P. gracilis* as equally possible.

2. Podandrogyne **decipiens** (Tr. & Pl.) Woodson, comb. nov.

Cleome decipiens Tr. & Pl. Prodr. Fl. Novo Gran. 75. 1862.
Gynandropsis decipiens (Tr. & Pl.) Pax & Hoffm. in Engl. & Prantl, Nat. Pflanzenfam. ed. 2. 17b:218. 1936.

COLOMBIA: *Cuatrecasas 13685.*

This specimen, collected by Dr. Cuatrecasas on the Cordillera Occidental, Depto. del Valle, at 300 m. alt., is of particular interest since it apparently represents the first collection of this species since the type. I have not been able to examine the type, collected at Quindio, and it is not represented in the Macbride collection of type photographs; but our specimen agrees so thoroughly with Triana and Planchon's description that there can be little doubt of its identity. Our specimen in the herbarium of the Missouri Botanical Garden is represented by two sheets bearing identical data, and is of interest from the standpoint of leaf variation. In one sheet, the leaves are broadly ovate and cordate, while in the other they are less broadly ovate and rounded at the base.

3. PODANDROGYNE **coccinea** (Benth.) Woodson, comb. nov.

Gynandropsis coccinea Benth. Pl. Hartw. 160. 1845.
Gynandropsis aurantiaca Turcz. in Bull. Soc. Nat. Mosc. 27^2:315. 1854.

COLOMBIA: *Hartweg 888; Linden 814; Funck & Schlim 1648* (photo). ECUADOR: *Mexia 8443, 8444; Steyermark 54230.*

This species is the Colombian and Ecuadorian counterpart of the Central American *P. chiriquensis,* from which, beside the more important key characters, it may be distinguished by the greater connation of the calyx lobes.

4. PODANDROGYNE **cernua** Woodson, spec. nov.

Herba ca. 1.5 m. longa aut fortasse basi frutescens omnino glabra. Folia longe petiolata lamina 3-foliolata foliolis brevissime petiolulatis ellipticis subcaudato-acuminatis basi latiuscule acutis 9–13 cm. longis 3–5 cm. latis membranaceis petiolo ca. 7–10 cm. longo. Inflorescentia terminalis racemiformis sat elongata secunda multiflora ebracteata; pedicellis usque 2.5 cm. longis; floribus inferioribus femineis superioribus masculis. Florum masculorum calyx campanulatus laciniis ca. tertia parte connatis acutis ca. 5 mm. longus glaber ruber apice purpureus; petala oblongo-spatulata ca. 1 cm. longa salmonea; androphorium eccentricum basi disco carnoso unilaterali cinctum ca. 1 cm. longum; antherae 6 ca. 8 mm. longae filamentis subaequilongis. Flores feminei desunt. Siliquae immaturae lineares glabrae stigmate sessili stipitatae basi glandula peristente instructae.

VENEZUELA: Mérida: between Los Corales and Las Cuadras, alt. 1490–3210 m., March 25, 1944, *J. A. Steyermark 55772* (Herb. Chicago Nat. Hist. Mus., TYPE).

It is rather remarkable that the two Venezuelan species of *Podandrogyne,* this and *P. macrophylla,* both are characterized by secund inflorescences. From the latter species, *P. cernua* differs not only in its palmately compound leaves, but in the larger flowers and linear, shortly stipitate fruits.

5. PODANDROGYNE **brachycarpa** (DC.) Woodson, comb. nov.

Gynandropsis brachycarpa DC. Prodr. 1:238. 1824.
Cleome brachycarpa Vahl, ex DC. loc. cit. 1824, nom. nud. in synon.
Gynandropsis hispidula DC. loc. cit. 1824.

Cleome hirsuta R. & P. ex DC. loc. cit. 1824, nom. nud. in synon.
Gynandropsis densiflora Benth. Pl. Hartw. 160. 1845.
Gynandropsis phoenicea Turcz. in Bull. Soc. Nat. Mosc. 27^2:316. 1854.
Gynandropsis adenocarpa Turcz. loc. cit. 1854.
Cleome puberula Tr. & Pl. Prodr. Fl. Novo Gran. 71. 1862.
Cleome densiflora Benth. ex Tr. & Pl. loc. cit. 72. 1862.
Cleome densiflora β pallens Pl. & Lind. ex Tr. & Pl. loc. cit. 1862.
Cleome Macrothyrsus Tr. & Pl. loc. cit. 1862.
Cleome lateralis Tr. & Pl. loc. cit. 73. 1862.
Cleome brachycarpa Vahl, ex Tr. & Pl. loc. cit. 1862.
Pedicellaria Lehmannii Hieron. in Engl. Bot. Jahrb. 20, Beibl. 49:20. 1895.
Pedicellaria Ulei Gilg, in Engl. Bot. Jahrb. 40:421. 1908, nom. nud.
Gynandropsis Ulei Briq. in Ann. Cons. & Jard. Bot. Genève 17:385. 1914.
Gynandropsis Mathewsii Briq. loc. cit. 387. 1914.
Gynandropsis Jamesonii Briq. loc. cit. 388. 1914.
Gynandropsis puberula (Tr. & Pl.) Macbr. in Field Mus. Publ. Bot. 11:22. 1931.
Gynandropsis hirsuta Moldenke, in Phytologia 1:5. 1933.
Gynandropsis lateralis (Tr. & Pl.) Pax & Hoffm. loc. cit. 1936.
Gynandropsis macrothyrsus (Tr. & Pl.) Pax & Hoffm. loc. cit. 1936.

This rather formidable synonymy has accumulated primarily because of the variability of texture and quantity of indument of the collected specimens, but also because of the bracteate inflorescence of certain of them and the ebracteate appearance of others. The species evidently is a rather common one from Colombia to Bolivia, and has been collected repeatedly. Although such questions are solved better through study of living plants, I have come to the conclusion through study of the exsiccatae enumerated below that *P. brachycarpa* is characterized by inflorescence bracts which are rather irregularly caducous, the latter propensity accounting for the seeming biotic variability. The bracts also, as is normal, decrease in size from base to apex of the inflorescence, so that inflorescences in a late state of development, in which the lower bracts have been lost, appear to be completely ebracteate.

A more important feature of the species, which apparently has been overlooked by most students, is the propensity for the lowermost flowers of the inflorescence to be hermaphrodite, and not pistillate only as in the other species. This character, together with the bracts, might suggest this species as being possibly the most primitive of the genus, at least from a structural standpoint.

COLOMBIA: *Haught 1953; Dryander 2081; Arbelaez & Cuatrecasas 6181; Lehmann 7437* (photo); *Triana s. n.* (photo); *Triana s. n.* (photo); *Triana s. n.* (photo); *Funck & Schlim 1407* (photo). ECUADOR: *Steyermark 54295; Steyermark 54867; Skutch 4542; Eggers 14907; Penland & Summers 111; Jameson 461* (photo). PERU: *Vargas 524; Macbride 4213; Schunke 266; Poeppig 1530; Weberbauer 6653; Ule 6430* (photo); *Mathews 193* (photo); *Pavon s. n.* (photo). BOLIVIA: *Buchtien 2219; Cardenas 707.*

6. PODANDROGYNE **gracilis** (Tr. & Pl.) Woodson, comb. nov.

Cleome gracilis Tr. & Pl. Prodr. Fl. Novo Gran. 74. 1862.
Cleome gracilis β turgescens Tr. & Pl. loc. cit. 1862.
Cleome porphyrantha Tr. & Pl. loc. cit. 71. 1862.

Gynandropsis gracilis (Tr. & Pl.) Macbr. in Field Mus. Publ. Bot. 11:22. 1931.
Gynandropsis porphyrantha (Tr. & Pl.) Pax & Hoffm. in Engl. & Prantl, Nat. Pflanzenfam. 17b:218. 1936.

COLOMBIA: *Cuatrecasas 8706; Goudot s. n.; Triana s. n.* (photo). ECUADOR: *Haught 2884; Steyermark 52853; Sodiro 68* (photo).

It is impossible for me to effect an absolute separation of this species and *P. brachycarpa*. Typically, as the preceding key suggests, the population which I call *P. brachycarpa* would appear amply distinct from the more northern *P. gracilis*. Amongst the specimens enumerated above, however, there is obvious intergradation, particularly with respect to indument, which might be construed as evidence of interspecific introgression through hybridization.

7. PODANDROGYNE **macrophylla** (Turcz.) Woodson, comb. nov.

Gynandropsis macrophylla Turcz. in Bull. Soc. Nat. Mosc. 27^2:314. 1854.

COLOMBIA: *Funck & Schlim 1210* (photo). VENEZUELA: *Steyermark 55821.*

Discussed previously with regard to *P. cernua.*

8. PODANDROGYNE **polychroma** Woodson, spec. nov.

Suffrutex erectus ca. 2 m. longus omnino glaber. Folia sat breviter petiolata lamina simplice late elliptica breviter acuminata basi late acuta ca. 20 cm. longa 10–11 cm. lata membranacea petiolo ca. 2.5 cm. longo. Inflorescentia terminalis racemiformis sat elongata secunda (?) multiflora ebracteata; floribus inferioribus femineis superioribus masculis; pedicellis usque 1 cm. longis. Florum masculorum sepala libera ovato-subreniformia obtusa ca. 5 mm. longa 7 mm. lata purpurea petala oblongo-obovata ca. 8 mm. longa rosea; androphorium eccentricum basi disco carnoso unilaterali cinctum ca. 1 cm. longum; antherae 6 ca. 8 mm. longae filamentis subaequilongis. Flores feminei desunt. Siliquae fusiformes glabrae ca. 10 cm. longae androgynophorio ca. 4 cm. longo basi glandula persistente instructo.

COLOMBIA: El Valle: Cordillera Occidental; vertiente occidental; Hoya del rio Sanquininí, lado izquierdo, La Laguna, bosques, 1,250–1,400 m. alt., Dec. 10–20, 1943, *J. Cuatrecasas 15578* (Herb. Missouri Bot. Gard., TYPE).

This species is utterly unlike any other known to me in the shape and color of the sepals, and particularly in the very large and conspicuous gland at the base of the fruiting androgynophores. Unfortunately, the one inflorescence is well past prime; consequently its description as secund must await verification.

9. PODANDROGYNE GLABRA Ducke, Archiv. Jard. Bot. Rio Jan. 5:115. *pl. 7, fig. 9.* 1930.

Gynandropsis orba Macbr. in Candollea 5:359. 1934.
Podandrogyne pubescens Asplund, in Sv. Bot. Tidskr. 30:266. *fig. 1.* 1936.
Podandrogyne orba Macbr. in Field Mus. Publ. Bot. 13^2:988. 1938.

COLOMBIA: *von Sneidern 1684.* ECUADOR: *Steyermark 52654; Sodiro 67* (photo). PERU: *Weberbauer 6760; Killip & Smith 26125; Killip & Smith 29594; Killip & Smith 29480.* BRAZIL: *Ducke 19701* (photo).

Podandrogyne pubescens differs from typical *P. glabra* only in its copious indument, as far as I am able to judge. But in several of the specimens enumerated above, which superficially appear glabrous, traces of pubescence may be found, particularly upon the petioles and peduncles. *P. pubescens* might possibly be interpreted as a variety of *P. glabra*, but I am not willing to maintain it as a species at the present time.

Explanation of Plate

PLATE 8

Figs. 1–5. *Podandrogyne chiriquensis:* 1, habit; 2, seed; 3, dehisced fruit; 4, staminate flower; 5, pistillate flower.

Fig. 6. *Podandrogyne coccinea:* staminate flower.

WOODSON—GYNANDROPSIS, CLEOME, AND PODANDROGYNE

MAIZE IN THE GREAT HERBALS[1]

JOHN J. FINAN[2]

INTRODUCTION

Maize is a plant of such overwhelming importance to the people who have grown it that its history is of special significance. There are so many kinds of maize, however, and it has been grown by so many people and for so long that its history is complex and difficult to piece together. The literature regarding it is scattered and fragmentary and mostly without illustrations. For one period, though, the record is fairly well documented. Beginning about a half-century after the discovery of America and extending through the seventeenth century, the plant is discussed in detail in the great European herbals. A careful examination and comparison of the material in these plant books with information on maize in the early chronicles of the New World will give us a reasonably accurate picture of what kinds of maize were current in Europe for the first few centuries after its introduction there. Moreover, as this study contributes to a more accurate understanding of maize, it should in numerous secondary ways illuminate the stories of the peoples who were growing it.

Most of the herbals are in Latin but all the major vernacular languages of Western Europe are represented. Discussions of plants in the herbals generally follow an outline formulated by the ancients. Separate sections in each discussion are devoted to various names for the plant, a description of it and its uses, medicinal properties, and place of origin. In the examination of the herbals, the information about the plant was abstracted systematically in tabular form on large ruled cards to allow for rapid and exact comparison of variations in different editions and among different herbalists. The great herbals are copiously illustrated with woodcuts, which present realistic pictures of the various types of maize seen by the herbalists.

The collection of herbals in the Missouri Botanical Garden Library, which includes almost every edition of every major herbal of the sixteenth and seventeenth centuries, was almost exclusively the source for the study of these plant books. In addition, the account in one of the first herbals to discuss maize, that of Bock (1539), was used in the form of a photostat copy supplied by the library of the Arnold Arboretum of Harvard University.

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[1] This work, done under a grant from Pioneer Hi-Bred Corn Co., Des Moines, Iowa, was originally presented as a master's thesis at Washington University. Faculty members of four departments of the University assisted the author: Dr. Edgar Anderson, of the School of Botany, who directed the project and helped in analyzing the biological significance of the material; Drs. William Bull, Herbert Dieckmann, Sherman Eoff, Bernard Weinberg, and the late Bateman Edwards, of the Department of Romance Languages, and Dr. Norman DeWitt, of the Department of Classics, all of whom assisted with textual problems and gave valuable suggestions on organizing the paper; and Dr. Horst Janson, of the Department of Art and Archaeology, who assisted with the examination of the woodcuts.

[2] Formerly Pioneer Hi-Bred Corn Co. Fellow in Washington University.

MAIZE IN POST-CONQUEST HISPANIC AMERICA

The significance of maize as a major crop—a staple food among the natives of the New World—led European explorers there to write about the plant in their reports. They make some mention of what it looked like and go into great detail about its uses and the customs and ceremonies associated with it. These reports are scattered, however, and only a brief summary of some of the major discussions of maize is presented here.

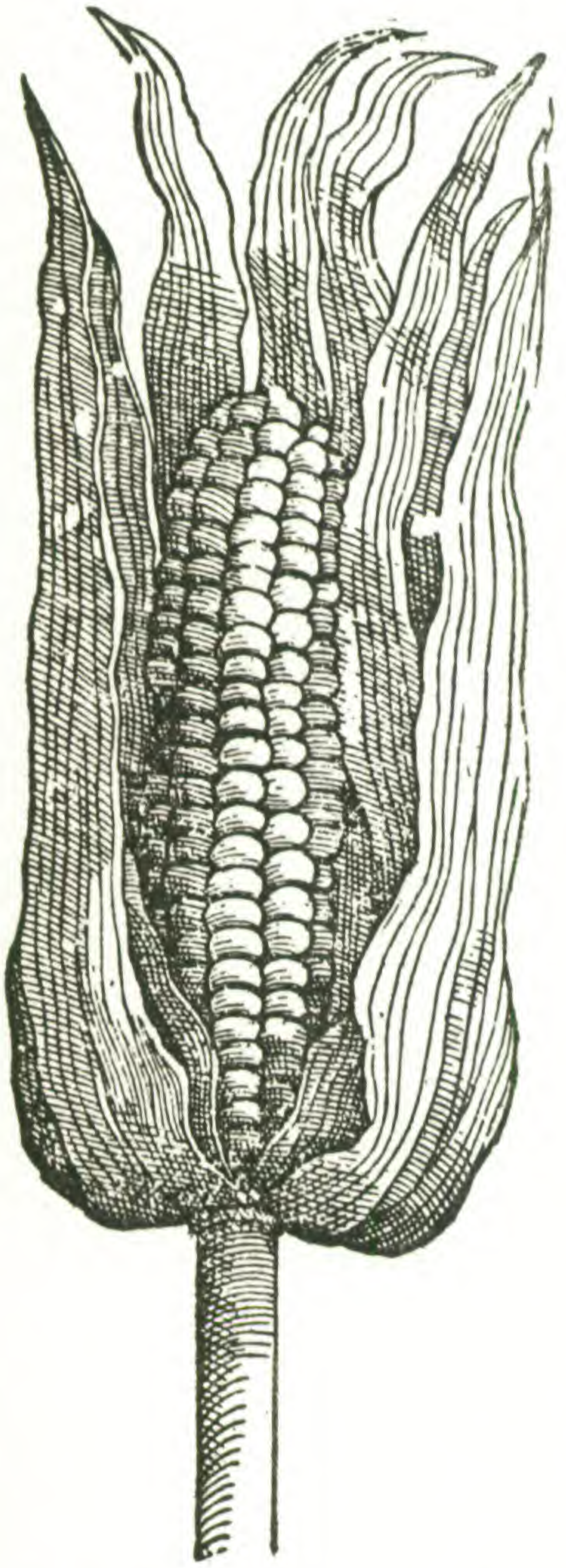


Fig. 1. The first illustration of maize published in Europe. From a seventeenth century translation of Oviedo's *Historia natural y general*, and reported to have been in the 1535 edition of his work.

Beginning with the first reports of Columbus, there are countless references to maize in the literature of exploration.[3] Almost all the major explorers mention the plant, but the first visitor to the New World to discuss maize in detail was a Spanish inspector of mines, Gonzalo Fernández de Oviedo y Valdés, who was sent to America in 1513[4]. The history of the Indies, which he compiled and published in 1526 and 1535,[5] contains an entire chapter on maize. And throughout his multi-volumed work, he gives a vivid picture of the place of maize in the life of the natives.

A contemporary of Oviedo, Francisco López de Gómara, who also visited the New World, and who, besides, received a great deal of material from Cortés,[6] includes detailed

[3]On his third voyage Columbus describes maize as "a seed which produces a spike like a cob, which I brought there, and now there is much of it in Castile;" —quoted by Salvador de Madariaga, *Vida del muy magnifico señor don Cristobal Colón*. Editorial in *Sudamericana*, p. 455. 1940.

The famous chronicler of Columbus' Travels, Peter Martyr, also reports of the plant as early as 1511: "This millet [maize] is a little more than a palm in length, ending in a point, and is about the thickness of the upper part of a man's arm. The grains are about the form and size of peas. While they are growing, they are white, but become black when ripe. When ground they are whiter than snow. This kind of grain is called *Maiz*."—*De Orbe Novo, The Eight Decades of Peter Martyr d'Anghera*. 1:64. Trans. from the Latin with notes and introd. by Francis Augustus MacNutt. New York and London, 1912.

[4]Miall, L. C. *The early naturalists*, p. 60.

[5]*La historia natural y general de las Indias yslas y tierra firme del mar oceano*. . . Sevilla.

[6]López de Gómara, Francisco. *Encyc. Brit.* 14:387. 14th ed. 1929.

accounts of maize in his *General History of the Indies* (1552). Another natural historian of the New World, Joseph de Acosta, who visited Peru in 1570 and Mexico in 1583,[7] published references to the maize of these regions in 1590.[8] In addition, there was a vast amount of material, not available to the Renaissance herbalists and only now being published, which contains a great deal of information on the plant. This has been obtained from *relaciones*, answers to a series of questionnaires sent out by the Spanish government, the first in 1577 and the second a quarter of a century later. There are items in both questionnaires inquiring about the grains of each region. A portion of these reports has been assembled and published in two collections.[9]

Piecing together the picture of what maize was like in the New World during the Conquest is difficult because of the frequently sketchy descriptions of the explorers. They were describing it to a world which had never seen it, and their descriptions are not precise, but general, and in terms which their readers could understand.

Oviedo used familiar comparisons in giving a picture of maize. The breadth of the maize stalk, he says, was either the size of one's thumb or the thickness of a calvaryman's lance, depending on the fertility of the soil. Its height he estimated as much higher than that of a man, and its leaves look like those of the common cane of Spain but "much longer and narrower, more flexible and greener." With more detail, he adds:[10]

> Each stalk produces at least one ear, and some two or three. There are about two hundred or more grains, depending on the size of the ear. Each ear is wrapped in three or four rather coarse leaves or coverings [husks], attached close to the grains, one on top of the other, and of the same texture as the leaves of the stalk.

Oviedo, speculating about the origin of the plant, suggests that it is the same as a plant described by the first-century Italian natural historian, Pliny. Indirectly he gives us more details about the corn plants he saw in the New World, as well as about some he saw in Europe:[11]

> As I am fond of reading Pliny, I shall repeat here what he says of the millet of India. I think it is the same as what we call "mahiz" in our Indies. Pliny says: "Ten years ago there came a millet from India which is black and has a large kernel. The stalk, like reeds, grows seven feet high . . . . It is the most fertile of all grains. One grain yields three *sextarii.* It should be sown in damp places." From this description . . . . [of Pliny] . . . . I would consider it to be maize because even though he remarks that it is black, maize in the New World

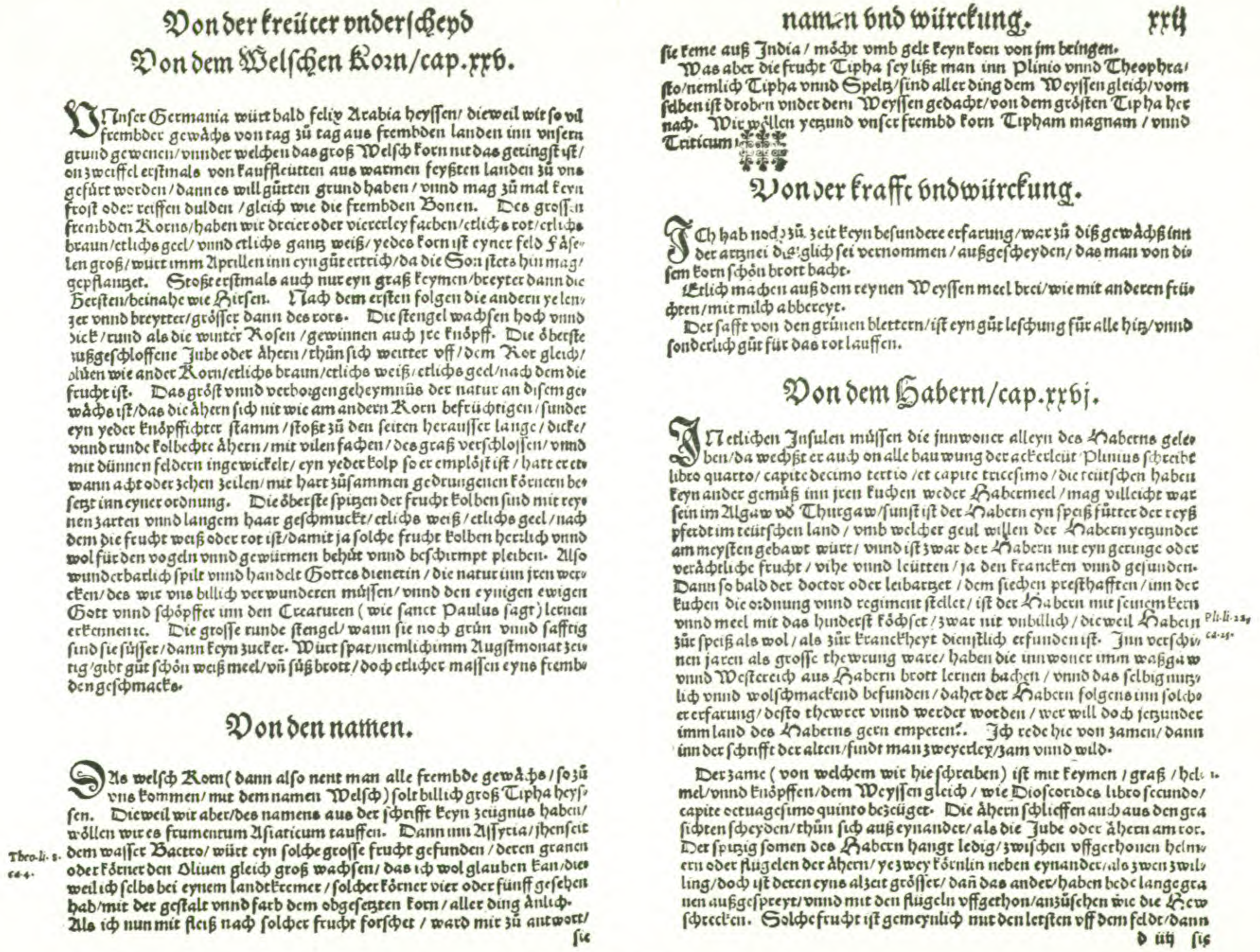
[7] Miall, *op. cit.*, p. 65.

[8] An old English translation was the oldest found available: Acosta, Ioseph, *The Naturall and morall historie of the East and West Indies.* Trans. by E. Grimestone. London, 1604.

[9] *Papeles de Nueva España, segunda serie, geografía y estadística.* Ed. by Francisco del Paso y Troncoso. 7 vols. Madrid, 1905; *Relaciones geográficas de Indias.* Ed. by Marcos Jiménez de la Espada. 4 vols. Madrid, 1881–1897.

[10] *Op. cit., Lib. 7, Cap.* 1, *Fol.* 72. Translation of this and other quotations from original texts made by author unless otherwise stated. See original passages in Appendix II.

[11] *Historia general y natural de las Indias* . . . . publ. by Real Acad. Hist. 1:268. Madrid, 1851.



Von der kreüter underscheyd
Von dem Welschen Korn/cap.xxv.

Unser Germania würt bald felix Arabia heyssen/ dieweil wir so vil frembder gewächs von tag zů tag aus frembden landen inn unsern grund gewenen/ unnder welchen das groß Welsch korn nit das geringst ist/ on zweiffel erstmals von kauffleutten aus warmen feyßten landen zů uns gefürt worden/ dann es will gůtten grund haben/ unnd mag zů mal keyn frost oder reiffen dulden/ gleich wie die frembden Bonen. Des grossen frembden Korns/ haben wir dreier oder viererley farben/ etlichs rot/ etlichs braun/ etlichs geel/ unnd etlichs gantz weiß/ yedes korn ist eyner feld Fäselen groß/ würt imm Aprillen inn eyn gůt ertrich/ da die Son stets hin mag/ gepflantzet. Stoßt erstmals auch nur eyn graß keymen/ breyter dann die Gersten/ beinahe wie Hirsen. Nach dem ersten folgen die andern yelenzer unnd breytter/ grösser dann des rors. Die stengel wachsen hoch unnd dick/ rund als die winter Rosen/ gewinnen auch jre knöpff. Die öberste ußgeschloffene Jube oder ähern/ thůn sich weitter uff/ dem Ror gleich/ blüen wie ander Korn/ etlichs braun/ etlichs weiß/ etlichs geel/ nach dem die frucht ist. Das gröst unnd verborgen geheymnüs der natur an disem gewächs ist/ das die ähern sich nit wie am andern Korn befrüchtigen/ sunder eyn yeder knöpffichter stamm/ stoßt zů den seiten herausser lange/ dicke/ unnd runde kolbechte ähern/ mit vilen fachen/ des graß verschlossen/ unnd mit dünnen feldern ingewickelt/ eyn yeder kolp so er emplößt ist/ hatt er etwann acht oder zehen zeilen/ mit hart zůsammen gedrungenen körnern besetzt inn eyner ordnung. Die öberste spitzen der frucht kolben sind mit reynen zarten unnd langem haar geschmuckt/ etlichs weiß/ etlichs geel/ nach dem die frucht weiß oder rot ist/ damit ja solche frucht kolben herrlich unnd wol für den vogeln unnd gewürmen behůt unnd beschirmpt pleiben. Also wunderbarlich spilt unnd handelt Gottes dienerin/ die natur inn jren werken/ des wir uns billich verwunderen müssen/ unnd den eynigen ewigen Gott unnd schöpffer inn den Creaturen (wie sanct Paulus sagt) lernen erkennen rc. Die grosse runde stengel/ wann sie noch grün unnd safftig sind sie süsser/ dann keyn zucker. Würt spat/ nemlich imm Augstmonat zeitig/ gibt gůt schön weiß meel/ vñ süß brott/ doch etlicher massen eyns frembden geschmacks.

Von den namen.

Das welsch Korn (dann also nent man alle frembde gewächs/ so zů uns kommen/ mit dem namen Welsch) solt billich groß Tipha heyssen. Dieweil wir aber/ des namens aus der schrifft keyn zeugnus haben/ wöllen wir es frumentum Asiaticum tauffen. Dann inn Assyria/ jhenseit dem wasser Bactro/ würt eyn solche grosse frucht gefunden/ deren granen oder körner den Oliuen gleich groß wachsen/ das ich wol glauben kan/ dieweil ich selbs bei eynem landtkremer/ solcher körner vier oder fünff gesehen hab/ mit der gestalt unnd farb dem obgesetzten korn/ aller ding änlich. Als ich nun mit fleiß nach solcher frucht forschet/ ward mir zů antwort/ sie

Theo.li.8. ca.4.

namen und würckung. xxij

sie keme auß India/ möcht umb gelt keyn korn von jm bringen.

Was aber die frucht Tipha sey lißt man inn Plinio unnd Theophrasto/ nemlich Tipha unnd Speltz/ sind aller ding dem Weyssen gleich/ vom selben ist droben unnder dem Weyssen gedacht/ von dem grösten Tipha hernach. Wir wöllen yetzund unser frembd korn Tipham magnam/ unnd Triticum

Von der krafft und würckung.

Ich hab noch zů zeit keyn besundere erfarung/ war zů diß gewächß inn der artznei dienstlich sei vernommen/ außgescheyden/ das man von disem korn schön brott bacht.

Etlich machen auß dem reynen Weyssen meel brei/ wie mit anderen früchten/ mit milch abbereyt.

Der safft von den grünen blettern/ ist eyn gůt leschung für alle hitz/ unnd sonderlich gůt für das rot lauffen.

Von dem Habern/cap.xxvj.

In etlichen Insulen müssen die innwoner alleyn des Haberns geleben/ da wechßt er auch on alle bauwung der ackerleüt Plinius schreibt libro quarto/ capite decimo tertio/ et capite tricesimo/ die teütschen haben keyn ander gemüß inn jren kuchen weder Habermeel/ mag villeicht war sein im Algaw vñ Thurgaw/ sunst ist der Habern eyn speiß fütter der reyßpferdt im teütschen land/ umb welcher geul willen der Habern yetzunder am meysten gebawt würt/ unnd ist zwar der Habern nit eyn geringe oder verächtliche frucht/ vihe unnd leütten/ ja den krancken unnd gesunden. Dann so bald der doctor oder leibartzet/ dem siechen presthafften/ inn der kuchen die ordnung unnd regiment stellet/ ist der Habern mit seinem kern unnd meel mit das hunderst köchset/ zwar nit unbillich/ dieweil Habern zůr speiß als wol/ als zůr kranckheyt dienstlich erfunden ist. Pli.li.22. ca.25. Inn verschinen jaren als grosse thewrung ware/ haben die innwoner imm waßgaw unnd Westereich aus Habern brott lernen bachen/ unnd das selbig nutzlich unnd wolschmackend befunden/ daher der Habern folgens inn solcher erfarung/ desto thewrer unnd werder worden/ wer will doch jetzunder imm land des Haberns gern emperen?. Ich rede hie von zamen/ dann inn der schrifft der alten/ findt man zweyerley/ zam unnd wild.

Der zame (von welchem wir hie schreiben) ist mit keymen/ graß/ helmen/ unnd knöpffen/ dem Weyssen gleich/ wie Dioscorides libro secundo/ capite octuagesimo quinto bezeüget. Die ähern schlieffen auch aus den gräsichten scheyden/ thůn sich auß eynander/ als die Jube oder ähern am ror. Der spitzig somen des Habern hangt ledig/ zwischen uffgethonen helmern oder flugelen der ähern/ ye zwey körnlin neben eynander/ als zwen zwilling/ doch ist deren eyns alzeit grösser/ dañ das ander/ haben bede lange granen außgespreyt/ unnd mit den flugeln uffgethon/ anzůsehen wie die Hewschrecken. Solche frucht ist gemeynlich mit den letsten uff dem feldt/ dann

d iiij sie

Fig. 2. One of the first discussions of maize by a European herbalist, Hieronymus Bock, in the *Neu Kreuterbuch* (1539).

is mostly dark purple or red. There is also white maize and much that is yellow and it might be that Pliny did not see all these other colors but only the dark purple which appears black. Maize has a stalk which, as he says, is like that of a reed and anyone who was not acquainted with the plant and had not seen it in the field before at full height would think it were a cane field. For the most part, maize [in the New World] is somewhat higher than the seven feet which Pliny describes. In some places it is very high, in others less so, depending on the fertility or goodness of the soil in which it is sown.

As for what he says about its being very high yielding, I have already pointed out that I have seen eighty, a hundred, and [even] a hundred and fifty faneagues harvested from one faneague planted. Pliny says that it is sown in humid places; the Indies are very humid. But to prove that maize needs to be planted in humid land or where there is a good supply of water, I mention that while Her Majesty, the Empress, was in Avila, during the time the Emperor was in Germany, I saw in that city, which is one of the coldest in Spain, inside a house a good plot of maize with stalks about ten hands high [80 inches high] as stout and as green and as beautiful as can be seen around here; near by was a well from which they watered it each day. I was really astounded, remembering the distance and difference in climate of this region from that of Avila . . . . The event took place in 1530 A. D.

An anonymous explorer who accompanied Cortés in his conquest of Mexico describes kernels with varying colors:[12]

The grain with which they make their bread is a kind of pea, and there is white, crimson, black and reddish. Planted, it produces a high cane like a half pike, which gives two or three ears where the grain is, as in Panizo or Panic grass.

Gómara describes the maize of Guatemala as being very large, and adds:[13]

Only one stalk grows from each grain. Often, however, one stalk bears two and three ears, and one ear bears 100, and 200, 400 and even as many as 600 grains. The stalk grows as high as a person and higher and is very thick. It bears leaves like our cane, but these are broader, longer, greener and softer. The plant matures in four months, on some lands in three, and on irrigated land in a month and a half, but this is not as good.

Acosta describes a similar plant:[14]

[Maize] grows upon canes or reeds; every one bears one or two grapes or branches, to the which the grain is fastened and although the grain is large, yet there are great many of them. In some clusters I have counted seven hundred grains. They must plant it with the hand one by one, and not very thick; it desires a hot and moist ground, and grows in great abundance in many places of the Indies. It is not strange in those countries to gather 300 *faneagues* or measures for one sown . . . . There is difference between maize varieties as there is among those of wheat; one is great and very nourishing, another small and dry, which they call *Moroche* . . . .

Although these explorers did not go into much detail about differences in maize varieties, they readily recognized the significance of the plant in the lives of the natives. They saw it used as a food in countless ways. Primarily, of course, they recognized its importance as a bread food. Oviedo entitles his chapter on maize "Concerning the Bread of the Indies Called Mahiz",[15] and he frequently uses the Spanish term for bread, *pan*, synonymously for *Mahiz*. Gómara explains in detail how maize bread was made:[16]

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[12] *Narrative of some things of New Spain*, p. 35. Ed. and trans. by Marshall H. Saville. The Cortés Society. New York, 1917. The original Spanish text has been lost, Saville's text being from a Spanish translation of the Italian of Ramusio.

[13] López de Gómara, Francisco. *La historia general y natural de las Indias, Lib.* 1, p. 289. 1552.

[14] *Op. cit., Lib.* 4, p. 254.

[15] *Op. cit., Lib.* 7, *Cap.* 1, p. 72.

[16] *Op. cit. Lib.* 1, p. 289.

They formerly did not have any wheat throughout the Indies, which are another world; [it would be] greatly missed here [in Spain] because of its extensive use, but, nevertheless, the natives of those regions [America] never felt nor do not feel the need for it, since they all eat bread made of maize . . . [To prepare] this bread for eating, they cook the grain in water, mash, grind and knead it; and they either cook it, wrapped in leaves in hot ashes (because they do not have ovens) or they roast it over live coals. Others grind the grain between two rocks like mustard, for they do not have mills. This is very hard work not only because of the hardness of the grain but because of the length of time it takes, which is not like that for making wheat bread. And so the women spend a part of each day at work preparing it; it loses its harsh flavor and it soon is ready. In three days it spoils and even decays. It stains and hurts the teeth a great deal, and for that reason they take great care in cleaning their teeth.

There were variations on the methods of making bread. Sometimes for native nobles and other persons of high rank the bread was made from red maize and pressed to a wafer-like thinness. Equally common as its use in bread was the roasting of maize ears, which is frequently mentioned by the explorers. A gruel of maize boiled and thinned out with water was eaten by the Indians of Mexico for breakfast and was used by the Spaniards there as a healthful food for the sick.[17]

The explorers seem to have been impressed by the uses of maize for alcoholic beverages among the Indians, as these are reported in detail. Oviedo describes how the maize beer *(chicha)* was made:[18]

All, for the most part, drink water, but no one dislikes wine. Rather, they are very fond of it. And they make as much *chicha* (which they call their wine) as they want, out of maize. This is their recipe for making it: they soak the maize and let it remain in water until it begins to germinate and swell up and some sprouts come out from that part of the grain which was attached to the ear. As soon as it has reached this point they cook it in good water, and after it begins to boil and to cook down they take from the fire the pot in which they cook it, and let it set until the grain settles. That day it is not ready to drink; but the second day it is more settled and they begin to drink some of it, although it is still somewhat thick. On the third day it is good and clear, because it is entirely settled. The fourth day it is even better, the color being like that of cooked Spanish white wine. It is an excellent beverage. The fifth day it begins to sour, and on the sixth it sours even more. On the seventh day it is vinegar and not fit to drink.

The kernels were frequently chewed by old Indian women and children to hasten the fermentation.[19] And Acosta[20] says it was a tradition among the Indians that the older were the women who did the chewing the stronger would be the liquor. Another type of wine was made from parched maize.[21] Revelry and drunkenness accompanied the drinking of these potions. As one of the *relaciones* said:[22]

[The Indians] drink so much [maize liquor] that it makes them drunk. In order to get drunk they have parties in private houses with dancing to drums and crude instruments. It is a custom among the Indians not to drink this liquor alone; rather, they have all the glasses in pairs, and one person must take a drink himself from one glass and give his companion a drink from the other.

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[17] Clavigero, D. F. S., *The history of Mexico* 1:433.

[18] *Op. cit.* 3:136. 1853.

[19] Vázquez de Espinosa, Antonio. *Compendium and Description of the West Indies.* Trans. by Charles Upson Clark, in Smithsonian Inst. Washington, Misc. Coll. 102:426. 1942. The original Spanish ms. is unpublished.

[20] Acosta, *op. cit., Lib.* 4, p. 256.

[21] Vasquez de Espinosa, *op. cit.*, p. 426.

[22] *Ciudad de la Paz* in *Relaciones geográficas,* 2:71–72.

And such carousing often went on for days.[23]

In addition to its staple use in bread, there were a number of special food uses for maize. Maize bread was sometimes made with eggs added[24] and sometimes walnuts were mixed with the maize flour.[25] Tamales were also prepared.[26] The Indians of Peru obtained a cooking fat and an oil from maize kernels,[27] and sugar was prepared from the juice pressed from the maize stalk.[28] Amazed at all of the uses to which maize was put by the Indians, Acosta confirms the remark of a Spanish viceroy that the New World was rich in two things: "maize and cattle." "He was right," adds Acosta, "for these two things serve them as a thousand."[29]

How much maize meant in the lives of the Indians is revealed in the reports from the explorers on its use in ceremonies, and on various native customs related to the plant. The Aztecs worshipped a god of maize,[30] Cinteotl, and maize was an acceptable offering to their gods,[31] especially white maize and maize wine.[32] A gruesome sacrificial ceremony of a maize offering is vividly described by Oviedo:[33]

> . . . before the feast, they collect many fasces of maize, and they put them around the sacrificial pile. First come the high priests of the devil . . . then the chief, and next in line each of the leaders according to his rank, who offer themselves in sacrifice. With some rock knives they cut their tongues and ears and genitals, and cover the maize with their blood. Afterwards, they divide [the grain] among themselves . . . and they eat it as though it were something very holy.

Small communion wafers were made of maize in Peruvian religious ceremonies to the sun.[34] The Indians of Nicaragua maintained chastity during the maize season, from sowing to harvesting.[35] In some marriage ceremonies the bride held in her right hand an ear of maize to signify that she would take care of the household and food.[36] So precious was maize considered in Mexico that any one who stole maize from a field became the slave of the owner of the field.[37]

Native methods of sowing are frequently reported in detail, including the account given by Oviedo and copied by Matthiolus (see below).

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[23] Acosta, *op. cit., Lib.* 4, p. 255.
[24] Clavigero, *op. cit.*, p. 212.
[25] du Pratz, L. P. *Histoire de la Louisiane,* 2:383.
[26] *Narrative of some things of New Spain,* p. 36.
[27] Acosta, *op. cit., Lib.* 4, p. 256.
[28] Von Humboldt, A. *Personal narrative of travels to the equinoctial regions of America during the years 1799–1804,* 2:400–401.
[29] *Op. cit., Lib.* 4, p. 256.
[30] Clavigero, *op. cit.*, p. 253.
[31] *Descripción de la Tierra Rucanas Antamarcas, Relaciones geográficas,* 1:207.
[32] *Relación de Caguasqui y Quieca, Ibid.* 13:126; and Oviedo, *op. cit., Lib.* 49, *Cap.* 4, p. 389. 1535.
[33] *Op. cit., Lib.* 42, *Cap.* 11, p. 98. 1855.
[34] Acosta, *op. cit., Lib.* 5, pp. 391–392.
[35] Oviedo, *op. cit., Lib.* 42, *Cap.* 11, p. 101. 1855.
[36] du Pratz, *op. cit.* 2:392.
[37] *Narrative of some things of New Spain,* p. 45.

Maize in the Great Herbals

Maize is reported in Europe very early after the Discovery. Columbus in his report on the Third Voyage writes that the plant was then growing in Spain.[38] And in the 1525 edition of Oviedo's *Historia,* there is a mention of maize growing near Madrid.[39]

Fig. 3. Woodcut of maize from the work of the Italian herbalist, Matthiolus (1570). Note the similarity between this illustration and fig. 1. At the right is a stalk that appears to be a stylized copy of the plant in Fuchs' cut (fig. 4).

Some time in the 1530's, maize began to attract the interest of the European herbalists, who, carrying on a medical tradition of almost 2000 years, published descriptions and uses of plants, chiefly those with medicinal properties. The discussions of maize in these great plant books give us a detailed and illustrated record of some of the European types of maize during the Renaissance. For the first thirty years in which maize is discussed in the herbals there is no mention that it had been brought in from America. Although reports of maize by the Spanish explorers and chroniclers were being published in Europe at the time, they were apparently slow in their spread over Europe. During this period, the general opinion among the herbalists was that maize had been brought into Europe from the Orient. It was not until 1570, with the herbal of the Italian Matthiolus (1570, p. 305), who had seen the text of Oviedo's *General and Natural History,* that an American origin for maize is suggested.[40]

Maize was first reported in the herbals in the work of the German herbalist, Jerome Bock (1539, fols. 21–22). He calls the plant *Welschen Korn* or "strange grain." The plant, he explains, is new in Germany and probably came from India:[41]

[38] See footnote 3.
[39] Von Humboldt, *op. cit.* 2:394.
[40] The two texts are compared below in the discussion of the Matthiolus herbal.
[41] See text in fig. 2.

> All foreign plants are called *Welsch* but this really should be called Typha. Because we have no written proof, we want to name it *Frumentum Asiaticum* [Wheat of Asia] because in Assyria . . . such a fruit is found whose grains or kernels grow as large as olives and this I can easily believe. I myself have seen four or five such grains at a country merchant's—grains similar in shape and color to those discussed here. When I made a thorough inquiry about such a fruit, I was told that it came from India. . . . One reads in Pliny and Theophrastus what the fruit Typha is: Namely Typha and Spelt are similar in all respects to wheat . . .

Bock describes a plant that bore ears of eight to ten rows with kernels either red, brown, yellow, or completely white. On the whole, Bock found the plant startling. He marvels at the long "threads"[42] that grow out from the ears and he suggests they function as a scarecrow device to keep birds and vermin from destroying the plant. He says it is mysterious how the plant is fertilized, for ears enclosed in many sheaths sprout from the sides. Bock remarks that the juicy stems of the plant are "sweeter than any sugar," and he prescribes the juice from the green leaves as a remedy for erysipelas. He does not include an illustration in this early edition.

For one to understand the full meaning of Bock's text, and that of the other herbalists mentioning maize, it must be remembered that the great herbals of the Renaissance were the culmination of a long tradition. Early in the history of peoples an interest is shown in plants for their medicinal uses. Among the Greeks, from whom western Europe has derived much of its heritage, this interest was concentrated in the rhizotomists, a class of plant-gatherers whose beliefs and traditions served as the basis for the herbal—a collection of descriptions of plants put together for medical purposes. The earliest such collections date from the second century B.C.[43] In the century preceding, however, a pupil of Aristotle, Theophrastus of Eresus, made a philosophic study of plants as plants and not merely for their medical applications. He included, nevertheless, in his *Enquiry into Plants*—as his only extant work is called—a description of the flora of the Mediterranean region, with accounts of the uses of a number of the plants.[44] As pointed out above, Bock attempts to associate maize with one of the plants that Theophrastus describes.

Two other ancient works were consulted by the Renaissance herbalists, who, in order to recover the old remedies, tried to associate the plants of western Europe with those mentioned in the ancient books.[45] The *Natural History* of Pliny (Secundus) was so influential throughout the Middle Ages that eighteen editions were printed in the fifteenth century and forty as late as the sixteenth.[46] Pliny, like Theophrastus, mentions a grain which the sixteenth-century herbalists attempt to identify with maize. The original passage from Pliny is quoted by Oviedo above.

Dioscorides, a Greek contemporary of Pliny, published an herbal *Materia*

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[42] The styles from the female ovaries of the corn plant, commonly called "silks."
[43] Singer, Charles. *From magic to science.* pp. 174–177.
[44] Arber, Agnes. *Herbals.* p. 7.
[45] Greene, E. L. Smithsonian Inst. Washington, Misc. Coll. 54:223.
[46] *Ibid.*, p. 158.

Fig. 4. The first illustration of maize in the herbals. From *De historia stirpium* of Leonhard Fuchs (1542).

medica, which became the medical bible of the Middle Ages. His work was of such consequence that "everyone who undertook the study of botany or the identification of medicine swore by his words. Even as late as the seventeenth century both the academic and the private study of botany may almost be said to have begun and ended with the text of Dioscorides."[47]

These early herbals were handed down to the Renaissance herbalists by copying and re-copying throughout the Middle Ages. Changes from the originals were chiefly additions, in some manuscripts, of glossaries listing the local dialectal names for the plants that were described. Some of the manuscripts had been copied and recopied for over a thousand years.[48]

The botanical renaissance was started in the first half of the sixteenth century by the "German Fathers of Botany," a group of herbalists among whom was Bock, whose works represent a return to nature.[49] The first of these was Otto Brunfels, whose *Herbarum vivae eicones*, published in 1530, is significant because of its realistic woodcuts which led the way for life-like portrayal of plants. He makes no mention of maize.

Bock, the second of the German fathers, whose chapter on maize has been discussed above, published his first herbal in German without illustrations. Later editions,[50] both in German and Latin, include the same material on maize but are illustrated with a stalk taken from the woodcut of maize in the work of Leonhard Fuchs, the next herbalist after Bock to discuss maize. (See fig. 7).

Fuchs' herbal, *De historia stirpium*, first published in Latin in 1542, presents a type of maize that is very much like that discussed by Bock.[51] His woodcut of the maize plant (see fig. 4), of folio size, is the first illustration of the whole plant to appear in Europe.[52] By 1542, maize had evidently become common in Germany, for Fuchs reports that "it is now growing in all gardens." He describes a plant with ears of eight to ten rows and bearing red, white, yellow, or purple kernels. Prop-roots (which might be expected to have sprouted from the lower nodes of the plant if it had been brought into Temperate Europe from some Tropical region of the New World) are neither mentioned in the text nor illustrated on the plant he portrays. Fuchs calls the plant *Frumentum Turcicum* and says that it was brought into Germany from Asia by the Turks, who were reported to have used it when other grains were scarce:[53]

> This grain, like many others, is one of those varieties which have been brought in to us from another place. Moreover, it came into Germany from Greece and Asia, whence it is called "Turkish grain," for today the huge mass of Turkey occupies the whole of Asia, and the Germans, noting the place of its origin, call it Turckisch korn.

[47] Sprengel, Kurt. *Historia rei herbariae*, I, as quoted by Greene ('00), p. 151.
[48] Singer, *op. cit.*, pp. 184–185.
[49] Arber, *op. cit.*, p. 52.
[50] *Kreuter Buch*, 1546, p. 249; 1560, p. 243. Tragus, *De stirpium* . . ., 1552, pp. 650–652.
[51] p. 824.
[52] A woodcut of maize is reported to have been included in the *Historia* of Oviedo (1535) according to Miall, *op. cit.*, p. 66. A check of the original texts of Oviedo's work in the Missouri Botanical Garden Library and in the Newberry Library does not reveal such an illustration. A reproduction of this cut in Ramusio (see footnote 44) is given in fig. 1.
[53] Fuchs, *op. cit.*, p. 824.

The term *Turcicum* during this period was probably used to mean "foreign." The Turks, attacking various parts of Western Europe, had introduced a number of new products there. Consequently, plants, animals and articles alien to a particular location were frequently assumed to have been brought in by the Turks and were labeled "Turkish."[54] From a similar misconception, the American bird, *Meleagris gallopavo gallopavo*, is commonly called a Turkey.[55]

Valerius Cordus, the fourth of the German herbalists, who was outstanding in plant description, is the first to recognize prop-roots in the maize plant:[56]

> It is supported by many fibrous roots from the sides, to which there are added other supports which grow out on all sides from the lowest node and are sent down into the ground. A cornfield is supported by these against strong wind.

Cordus' text, illustrated by a stalk copied from the cut of Fuchs, reads like a modern taxonomic description. He describes the morphology of the plant in fine detail. The ears have eight to ten rows and bear kernels that are either golden or yellow, and he says that an extraordinary type was found with red and black kernels. Cordus makes no mention of the origin or uses of the plant. By the name *Triticum Bactrianum*, which he calls maize, he associates the plant with the *Triticum* of Theophrastus.[57]

Two other German herbalists, whose works appeared at the end of the sixteenth century, present discussions of maize. A pupil of Brunfels, Tabernaemontanus, whose German name was Jacob Dietrich of Bergzabern, produced an herbal, *Neuw Kreuterbuch* in 1588, in which he describes two types of maize.[58] He discusses each in a separate chapter: one entitled *Frumentum Turcicum*, the other *Frumentum Indicum*. The first type has eight to ten rows with red, white, yellow, or purple kernels. It has no prop-roots (as might occur in plants brought in from the tropical regions of America), and its possible origin is not mentioned. The second type, labeled *Frumentum Indicum*, has broader leaves and ears with higher row numbers, and bears several rows of prop-roots. It has kernel colors of black, brown, white, yellow, and purple. This plant, Tabernaemontanus says, was brought from the New World via Spain. Twenty-three woodcuts are presented in Chapter IV of the herbal: one of an entire plant, four of individual ears to illustrate the first type of plant, one of the plant of *Frumentum Indicum*, and seventeen of its type of ears.

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[54] Information supplied by Dr. Horst Janson, of the Washington University department of art and archaeology, who is making a cultural study of the period.

[55] Information supplied by Dr. Hampton Carson, Washington University department of zoology. Fuchs uses a number of terms still in use today to describe the corn plant and other grasses. The word *culmus*, modified from the Greek *calamos*, from which comes our term "culm", is his word for the stems of grass-like plants. In an introductory glossary of "difficult" terms, he defines a spike as that which a culm bears at its summit, and in accordance with this definition, applies the term to the entire corn tassel which today is known as a panicle. (See Greene, *op. cit.*, p. 275.)

[56] *Annotationes*, p. 112. 1561.

[57] *Op. cit.*

[58] 1:758–764.

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Figs. 5–7. Reduced copies of the original cut of Fuchs' (fig. 4): Fig. 5. Reduction in the Fuchs herbal of 1545, copied in reverse of the original. Fig. 6. Reduction in the Fuchs herbals of 1549, 1551, and 1553, in reverse of fig. 5 and probably a copy from it. Fig. 7. Copy in the herbal of Bock (1546).

Two years earlier, Joachim Camerarius published an edition of the herbal of the Italian Matthiolus.[59] In this work Camerarius presents a dwarf maize plant to illustrate the text (see fig. 10). This is discussed below.

The herbal in the Low Countries centered around the cooperative work of three herbalists.[60] The first and most famous of these, Rembert Dodoens (in Latin, Dodonaeus), published his *De frugum historia* in 1552, and later editions in 1566, 1583, and 1616. In all of his editions Dodonaeus describes an ear of eight to ten rows, bearing, according to various editions (see Table III), either red, white, yellow, brown, or purple kernels. In the editions of 1566 and 1616 he says the stalk is five to seven feet high and bears three to four ears. His material on the origin and uses of maize differs in the various editions. In the edition of 1552, he calls maize *Milium Indicum,* associating it with the plant of Pliny, but adds:[61]

> This season it is called Turkish or Saracen grain because it is believed to have been brought in from Asia or Greece which are under the power of the Turks.

Bread made from this grain, he says, is binding and offers no nourishment to the body.

In the edition of 1566, he disagrees with Valerius Cordus' name for the plant, *Triticum Bactrianum,* and points out that Pliny spoke of a grain whose size would equal "one of our ears." He quotes some of the ancient descriptions and concludes:[61]

> Turkish corn is unlike these—it is not *Triticum Bactrianum,* but should be given a new name *Triticum Turcicum.* Some day some Oedipus will point out its ancient name or be able to show that it was described somewhere by the ancients or was at least known to them.

In this edition he presents the first original drawing of the maize plant since that of Fuchs in 1542 (see fig. 8). In the editions of 1583 and 1616, he denies an Oriental origin and says maize was brought in from the New World:[62]

> By no means [did it come] from Asia which is subject to the Turkish Emperor (as is commonly believed) or from the Orient, but from the West—from America and neighboring islands brought first into Spain and then into other states of Europe.

Another Low Country herbalist and a close friend of Dodonaeus,[63] Jules-Charles de l'Escluse (Clusius), edited the *Exoticorum libri decem* (1605), which included material of the New World chroniclers, García de Orta, Christophorus a Costa, and Nicolaus Monardes. In discussing the bread of the New World, Monardes presents a short paragraph on maize (see below).

The chief work of Mathias de l'Obel (Lobelius), the third of the Belgian herbalists, was *Plantarum seu stirpium historia* (1576), which was translated into Flemish in 1581 under the title *Kruydtboeck.* In this last work l'Obel presents a woodcut of a maize plant with six rows of prop-roots and labels it Indian corn

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[59] Matthiolus, Petrus, *De plantis epitome . . . aucta et locuplelata, a D. Ioachimo Camerario.* 1586, p. 186.
[60] Arber, pp. 79–92.
[61] *Op. cit.,* p. 35.
[62] *Op. cit.,* p. 509.
[63] Arber, *op. cit.,* p. 82.

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Fig. 8. Illustration of maize in the 1566 edition of the herbal of Dodonaeus.

Fig. 9. This cut, in the herbal of l'Obel (1581), is the first to illustrate prop-roots.

(see fig. 9). He distinguishes this from Turkish Corn, which he illustrates with the cut in the Dodonaeus edition of 1566. He describes ears with colored kernels similar to those reported by previous herbalists (see Table III) and does not go into detail about specific differences between the two plants. He disagrees with the statement of the Italian herbalist Matthiolus that maize came from America because, he says, the plant was mentioned by Pliny and others of the ancients who had never been to America.[64] Later (1605), he mentions a New World origin.

The most outstanding of the Italian herbalists, Petrus Matthiolus (Pierandrea Mattioli), was apparently the first of the European herbalists to have seen the literature of exploration. He is the first of the herbalists to deny an Oriental origin for maize and to suggest that the plant had been brought into Europe from

[64] *Op. cit.*, pp. 50–51.

America.[65] In his edition of 1570, where he first discusses maize, he says:[66]

> This type of grain, which they wrongly call *Turcicum*, can be numbered among the varieties of wheat. [It has been named] incorrectly, I say, because it ought to be called *Indicum*, not *Turcicum*, for it was first brought from the West Indies, not out of Turkey and Asia, as Fuchs believed.

Matthiolus was evidently influenced in this belief by the text of Oviedo. He includes in his discussion Oviedo's account of the methods used by the Indians to sow maize:

OVIEDO, 1535	MATTHIOLUS, 1570
five or six Indians stand . . . a step away from each other in a row and with a stick or macana [wooden sabre edged with sharp flint] they strike the earth, shake the stick in order to open up the earth and then take the stick out. In the hole they throw with their left hand four or five grains of maize which is taken from a small bag tied about the neck. With his foot he closes over the hole containing the grains lest parrots or other birds eat them. Then they take another step forward and do the same thing, proceeding throughout the field in the same way. All the Indians sow in a row until they arrive at the end of the piece of land they are sowing [continuing thus] until they have finished the whole field. (folios 71–72).	The Indians sow this seed, which they call Malitz, in this way. A number of them, in a straight line, at equal distances, go down into the field. Then they make a hole with a sharp stick in their right hand and with their left hand they throw in four or five grains in the hole covering it over with their foot lest parrots eat the seed. So with measured step backwards, they sow the whole field with grain. But before they entrust the seed to the ground they soak it in water for two days, and do not sow it unless the ground has been previously rained upon. [The plant] sprouts within a few days and is harvested in India in 4 months. (p. 305).

The last three sentences in the above excerpt from Matthiolus indicate that he had seen other sources, besides Oviedo, in the literature of exploration. The maize ear which Matthiolus illustrates is very similar to that found in the Ramusio translation of Oviedo[67] and, according to one student,[68] was in the original. Matthiolus describes ears with red, black, white, brown, purple or yellow kernels and having eight to ten rows. He calls the plant *Frumentum Indicum* and gives *malitz*[69] as the name for the plant in the New World. He also refers to a 40-day corn, and a two-month corn, both of which are mentioned widely in the literature of exploration. Later editions of Matthiolus (see bibliography) include for the most part the same text.

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[65] The Spanish herbalist Monardes, describing the flora of the New World, reports maize growing in America in his herbal of 1569 (see footnote 71). Because he does not describe or illustrate the plant or associate it with the common names for it in Europe, the material differs very little from other references in the literature of exploration.

[66] *Op. cit.*, p. 305.

[67] *Della naturale et generale historia dell'Indie, dove si tratta dell'agricoltura.* Venice, 1606, III, *Lib.* 7, p. 110.

[68] Miall, *op. cit.*, p. 61.

[69] Matthiolus probably misread the "h" of *mahiz* for an "l". The modern term has been studied in detail: "The word 'maize' is first recorded by Oviedo as the word for corn in the Cuban dialect of Arawak and [Oviedo] gives the original form in two spellings: '*maisí*' and '*majisí*' . . . [The phonetic interpretation of these spellings] is that the word starts off with *mah-*, which is followed by *-hi-* (this syllable in colloquial Spanish reduced to the second member of a diphthong), and the word is then closed by a third and final syllable *-si-*. By giving two spellings Oviedo makes it possible to know exactly what the pronunciation was. Though the Arawak language has for centuries been dead in the islands, there are Indians on the mainland of South America, for instance, in Guiana, who still speak a different dialect of it, and in their dialect, if we look for the

Castor Durante, another Italian herbalist, seems to have taken much of his texts from Matthiolus.[70] He labels his discussion *Grano d'India* (Grain of India) and, writing of the use of maize in the New World, quotes from Matthiolus. Durante describes an ear of eight to twelve rows, with red, white, and yellow kernels.

The Spanish herbalists, describing for the most part the flora of America, include the maize of the New World. The first of these, Nicolaus Monardes, published in 1569 his *Historia medicinal*, a work without illustrations and containing only a general reference to maize:[71]

> . . . bread is made of maize . . . They grinde it, and with water they knede it, and in a frying panne of earth they bake certain cakes which they make of it, and it must be eaten freshe, as soone as it is made; for being dry it is sharpe and troublesome to swallow down, and doeth offende the teeth . . .

Another Spanish herbalist, Francisco Hernández,[72] presents a detailed picture of the uses of maize in Mexico, giving much the same information that is in the literature of exploration. For the first time in the herbals, Hernández uses the Aztec name for maize, *tlaolli*, and describes it as having black, white, purple, dark blue, golden yellow or mixed-colored kernels. To illustrate his herbal he uses woodcuts taken from the l'Obel herbal of 1581.

Portuguese herbalists chiefly describe the flora of Portuguese dominions in the Orient and do not make reference to maize.

Maize is first mentioned in Switzerland in the herbals of Caspar Bauhin and of his brother Jean. Caspar's discussion of the plant in his *Phytopinax* (1596, p. 55) and *Pinax* (1623, pp. 24–26) is chiefly an attempt at the systematization of the descriptions of previous writers. He includes a description of a plant (1623, p. 25) with grains of "tender infolded skin", which might indicate pod corn. His brother Jean treats maize in somewhat the same way,[73] presenting a compendium of previous descriptions. Another Swiss student of plants, Konrad Gesner, had projected an herbal but it was not finished before his death. The 1500 drawings he prepared for the work were sold to the German herbalist Camerarius[74] and one of these may be the source of the woodcut of maize in Camerarius' herbal of 1586 (see fig. 10).

There were very few herbals compiled in France, and most of them are translations.[75] The few original French works deal almost entirely with pure systematic botany and, as far as I know, do not discuss maize.

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word for corn, we find *marise*." Quoted from: Harrington, John P. Origin of the word "maize." *Wash. Acad. Sci. Jour.* 35:68. 1945.

[70] *Herbario Novo.* 1602, pp. 217–218; 1617, pp. 217–218; *Hortulus Sanitatis.* 1609, pp. 397–399.

[71] Frampton, John. *Ioyfull newes out of the new-found worlde,* p. 104. The Spanish original was not available.

[72] *Rerum medicarum Novae Hispaniae, Thesavrvs . . . .* pp. 242–247.

[73] *Historia plantarum,* 2:453–454. 1651.

[74] Arber, *op. cit.,* pp. 110–111.

[75] *Ibid.,* p. 119.

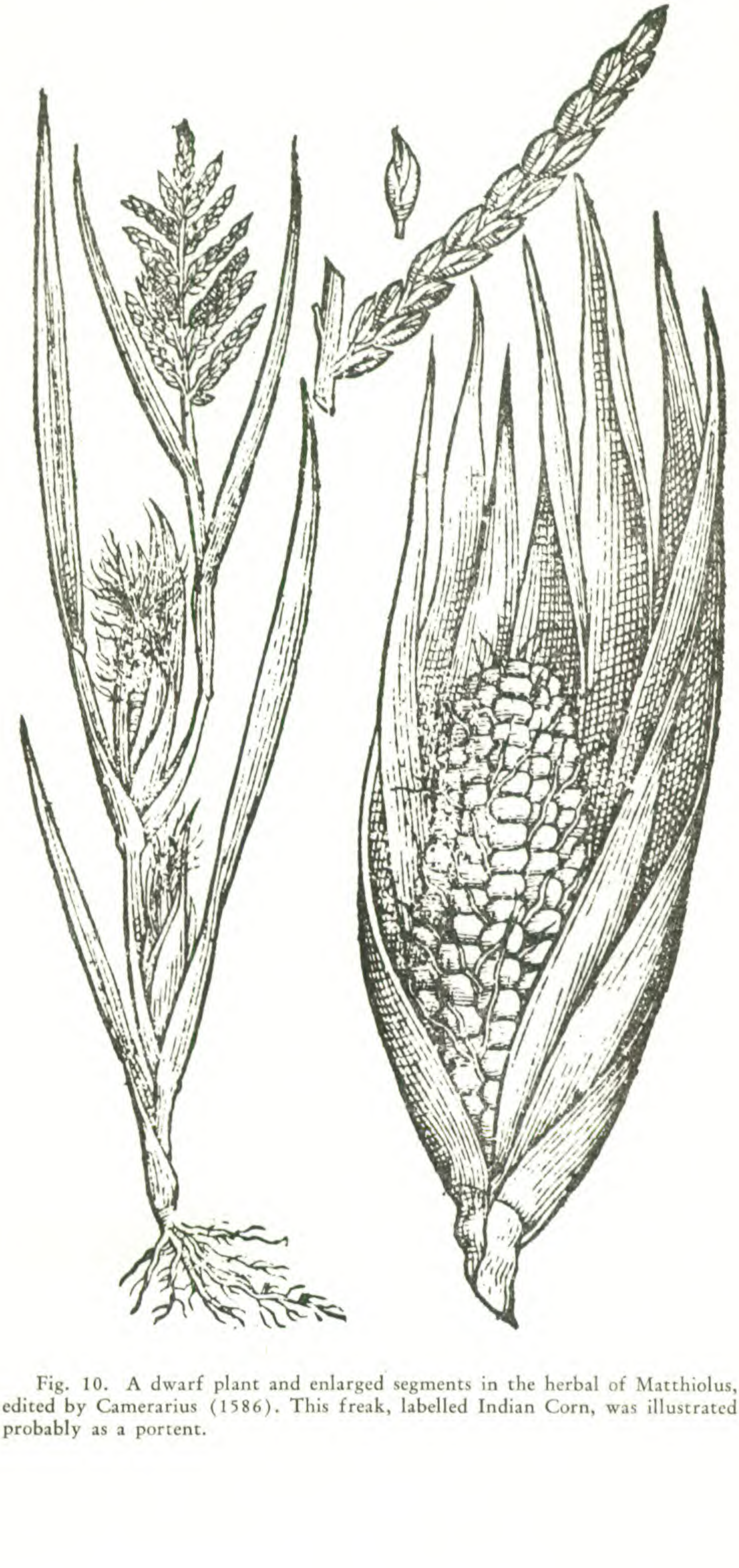

Fig. 10. A dwarf plant and enlarged segments in the herbal of Matthiolus, edited by Camerarius (1586). This freak, labelled Indian Corn, was illustrated probably as a portent.

The first discussion of the plant in England is in a translation of the *Cruydeboeck* of Dodonaeus[76] by Henry Lyte in 1578.[77] The *Herball* of John Gerarde,[78] the most famous of the English herbalists, is also a translation of Dodonaeus (*Pemptades,* 1583), arranged according to l'Obel. Gerarde adds, however, some original material in his discussion of maize. He says he has grown maize in his own garden and points out in "English it is called Turkey corne and Turky wheate." He suggests that the plant came from both America and Asia:[79]

> These kinds of graine were first brought into Spaine, and then into other provinces of Europe out of Asia which is the Turkes Dominions, as also out of America and the Ilands adioyning from the east and west Indies, and Virginia and Norembega, when they use to sowe or set it, and to make bread of it where it groweth much higher than in other countries.

He describes a maize ear which is of eight to ten rows and bearing red, white, yellow, or purple kernels. Four woodcuts from the 1588 edition of the herbal of Tabernaemontanus illustrate the text. The woodcut labeled *Frumentum Indicum* by Tabernaemontanus in his herbal of 1588 is here labeled *Frumentum Asiaticum,* Corne of Asia; but the cut which Tabernaemontanus labeled *Frumentum Turcicum* bears also that label in Gerarde's work.[80] In addition, Gerarde presents six woodcuts of ears from the Tabernaemontanus herbal with their original captions. In the 1636 edition of the *Herball,* Gerarde revises his original statement concerning the origin of maize:[81]

> These kinds of grain were first brought into Spaine, and then into other provinces of Europe: not (as some suppose) out of Asia Minor, which is the Turks Dominions; but out of America and the Islands adioining, as out of Florida, and Virginia or Norembega, where they use to sow or set it or make bread of it, where it grows much higher than in other countries.

John Parkinson, a later herbalist, discusses two types of maize in his *Theatrum Botanicum*:[82] (1) "*Frumentum Indicum vel Turcicum vulgare,* the usuall Indian or Turkie wheate," and (2) "*Frumentum Indicum alterum sive minus,* the other lesser Indian wheate." The first, which he says came "from the East and West Indies," is of six to ten rows and has blue, white, or yellow kernels and the plant bears two or three ears. This plant illustrated by the cut from the 1566 edition of the herbal of Dodonaeus (fig. 8) was, according to Parkinson, prevalent in England. It was without prop-roots. Parkinson points out that the maize plant with prop-roots illustrated in the herbal of l'Obel of 1581 is different from the plant he describes:[83]

> Lobel expresseth the figure of another sort as he thinketh because as hee saith it grew greater and higher, and the roote grew greater, *and with more separate tufts,* the roote not differing in anything else; but I thinke it no specificall difference, not understanding by any that it is taken for another sort, and, therefore, I have omitted it.

[76] *Posteriorum trium . . . de stirpium historia,* etc. 1554.
[77] *A nievve herball,* pp. 463–464.
[78] *The herball or generall historie of plantes.* 1597.
[79] *Ibid.,* p. 77.
[80] *Ibid.,* p. 75.
[81] *Ibid.,* p. 82.
[82] 1640, pp. 1138–1139.
[83] *Ibid.,* p. 1139.

The second type, Parkinson says, is "not halfe so high or great, the ears likewise are not halfe so bigge." This plant, he adds, is "a stranger, and seldome seene with us."[84] Parkinson's theory of the origin of the plant is especially interesting because he observed a fact—that maize cannot grow wild—which has stimulated modern biological interest in the plant:

> Matthiolus, Dodonaeus, Lugdunensis and others who condemne Fuchsius for calling it ***Frumentum Turcicum,*** according to his countries dialect are found more just to be blamed themselves, for no doubt but this very ***Indian*** Wheate which plentifully is found to grow in all the tract of the West ***Indies,*** yet not found naturall in any place, but planted everywhere by the natives, & is the same with Theophrastus and Pliny their ***Frumentum*** or ***Triticum*** and ***Milium Bactrianum Indicum.***[85]

That Parkinson had seen the work of Acosta is evidenced by the following statement:[86] " . . . Acosta saith the Spaniards in the Indies or the Indians call maize *Moroche;* the drinke made of *Maiz* is generally in the Indies called *Chicha,* but by some *Acua.*"

Then, speaking of the "Vertues" of the plant, Parkinson writes:[87] ". . . Acosta saith that by feeding too much on maize it engenders grosse blood, which breedeth itches and scabbes in those that were not used to it."

TABLE I

NAMES IN THE HERBALS FOR MAIZE

Welschen Korn
- Bock, 1539

Frumentum Asiaticum
- Bock, 1539
- Gerarde, 1597

Frumentum Turcicum (and variations)
- Fuchs, all eds. 1542–'95
- Bock, 1546, '52, '60
- Lonicerus, 1551
- Dodonaeus, 1563, '66, '78, '83, '86, 1644
- Cordus, 1561
- L'Obel, 1576, '91, 1605
- Tabernaemontanus, 1588, 1613, '64
- Bassaeus, 1590
- Gerarde, 1597, 1636
- Durante, 1602, '09, '17
- Parkinson, 1640
- Chabraeus, 1666, '77
- a Turre, 1685
- Matthiolus, 1696

Triticum Bactrianum
- Cordus, 1561

Frumentum Indicum (and variations)
- Cordus, 1561
- Matthiolus, 1570, '71, '83, '86, 1674, '96
- L'Obel, 1576
- Dodonaeus, 1586
- Camerarius, 1586
- Tabernaemontanus, 1588, 1613, '64
- Bassaeus, 1590
- Durante, 1602, '09, '17
- Parkinson, 1640
- Bauhin, 1658
- Boccone, 1674

Milium Indicum (Plinianum)
- Dodonaeus, 1552, '53, '54
- L'Obel, 1591, 1605

Maizium (and variations)
- Matthiolus, 1570, '83, '86, '98, 1611, '96
- Monardes, 1596
- Dodonaeus, 1583
- Cesalpinus, 1583
- Tabernaemontanus, 1588, 1613, '64
- Camerarius, 1586
- L'Obel, 1591, 1605
- Durante, 1602, '09, '17
- Clusius, 1605
- Gerarde, 1636
- Hernández, 1651
- Bauhin, 1658
- a Turre, 1685

Tlaolli
- Hernández, 1651

Triticum Peruvianum
- Chabraeus, 1666, '77

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[84] *Ibid.,* p. 1138.

[85] *Ibid.* Parkinson's reference to "Lugdunensis," above, is not clear. The French editions of Matthiolus (1561 and 1572) were published at Lyons.

[86] *Ibid.,* p. 1139.

[87] *Ibid.*

TABLE II

PLACE OF ORIGIN OF MAIZE ACCORDING TO THE HERBALS

India
- Bock, 1539
- Lonicerus, 1551

Greece or Asia held by the Turks
- Fuchs, 1542–'95 (all eds.)
- Lonicerus, 1551
- Dodonaeus, 1552, '63, '66, '78, '86, 1644
- Gerarde, 1597
- Bauhin, 1658

Turkey
- Bock, 1546, '52, '60

New World
- Matthiolus, 1570, '83, '86
- Dodonaeus, 1583, 1616
- Camerarius, 1586
- Gerarde, 1597, 1636
- Durante, 1602, '09, '17
- L'Obel, 1605
- Bauhin, 1658

New World via Spain
- Dodonaeus, 1583, 1616, '44
- Tabernaemontanus, 1588, 1613, '64

TABLE III

COLORS OF KERNELS

Herbal	Red	Black	Brown	Blue	White	Yellow	Purple
Bock, 1539–60 (inc.)	X		X		X	X	
Fuchs, 1542–95 (inc.)	X				X	X	X
Lonicerus, 1551	X				X	X	X
Dodonaeus, 1552	X				X	X	X
1563	X		X			X	
1566	X				X	X	X
1578	X		X		X	X	
1583, 1616	X				X	X	X
1586			X		X	X	
Cordus, 1561	X	X				X	
Matthiolus, 1570	X	X			X	X	X
1571		X	X		X		
1583		X	X		X	X	X
1586	X		X		X	X	
1696	X		X		X	X	
L'Obel, 1576		X					
1581	X		X			X	
1605				X			X
Camerarius, 1586	X	X			X		
Tabernaemontanus, 1588, 1613, '64							
Indicum	X	X	X	X	X	X	X
Turcicum	X				X	X	X
Bauhin, 1591					X		
1596	X		X	X		X	X
1651				X		X	X
1658					X	X	X
Gerarde, 1597, 1636	X				X	X	X
Durante, 1602, '09, '17	X				X	X	
Parkinson, 1640				X	X	X	
Hernández, 1651		X		X	X	X	X
Chabraeus, 1666, '77		X			X	X	X

WOODCUTS OF MAIZE IN THE HERBALS

Most of the Renaissance herbals studied here contain one or more woodcuts of maize. They generally accompany discussions of the plant in the texts and give us a rather clear picture of some of the types of maize in Europe in the sixteenth century. The illustrations are extremely realistic. They are not like those handed down from the Middle Ages, which, after being copied over and over again for hundreds of years, show only vague outlines of the original plants. Such a tradition ended when Dürer, and other great Renaissance masters, used the woodblock as a serious medium for their art. By their precision and realism they stimulated other competent artists to draw for the blocks of the herbalists.[88] They present plants in their natural state and with their individual peculiarities. Some of the artists went to extremes of realism. One, for example, went so far as to include the wilted leaves and bent stems of the herbarium specimens he used as models.[89]

Realistic as the woodcuts are, they supply us with much information about corn of this period, which is not in the herbal texts. Some characteristics, only recently found significant in classifying the plant, are presented clearly in the prints. These include ear shape, presence or absence of prop-roots, and "flag leaves" (the corn-breeder's nickname for leafy bracts [see Brown and Anderson, '47]), types of tassel branching, breadth of leaves, and other features. The herbalists, of course, did not describe these characteristics precisely for they had neither the scientific knowledge nor terminology necessary, nor the intention to do so. The function of most of the herbals was not to further the new science of botany or taxonomy, but to allow readers to associate the plants of their locality with those used in the ancient medicines. Therefore, to us who study the morphology of maize of this time, the cuts are especially important. Much that the herbalists did not describe in words, they have handed down to us through these drawings.

Despite their realism, the woodcuts are not exact depictions. There were some technical limitations in their making which prevented complete naturalism. It was difficult, for example, to present very fine detail of plants both because of the thickness of the woodcut line and the lack of pains taken in printing. The line was about 250μ—a breadth that would not allow the drawing of hairs, stamens, or parts of small florets less than 1–2 mm. in diameter.[90] Besides, the cuts were intended for mass printing to illustrate books, and detail was not given the same careful attention as in cuts for single prints. Fine features of the corn plant, such as tassel spikelets, suffered as a result. It was also hard to draw round features on the rectangular block. In many herbals, trees are drawn with square crowns,[91] and in some drawings of maize, such as in fig. 8, the long lateral leaves are bent at the sides and the roots squared off unnaturally.

The prints also have some errors. Drawn in a period when plant sexuality was not understood, the silks on the ears in almost all prints come out from the

[88] Arber, *op. cit.*, p. 202.
[89] Hans Weiditz, the artist for the *Herbarum vivae eicones* of Otto Brunfels (1530).
[90] Church, A. H. Brunfels and Fuchs. Jour. Bot. 57:233–244.
[91] Arber, *op. cit.*, p. 215.

tips of the cobs, rather than from each kernel. As pointed out above, one herbalist suggested that the silks functioned as a "scare-crow" device to keep away preying birds! In Fuchs' cuts (fig. 4) the top two leaves on the second shoot from the right are drawn opposite instead of the natural alternate arrangement. Such errors served a useful purpose in this study in revealing copies and are discussed in more detail below. Many of them can be explained partially by the lack of knowledge of the corn plant at that time, and partially by a possible lack of cooperation between the various woodcut craftsmen. Three different craftsmen sometimes worked on each cut: the artist who made the original drawing, another craftsman who drew it on the block, and a sculptor who cut out the wood.[92] When there was little close-working among the three, a misunderstood detail might have been misrepresented.

It was a common practice among the herbalists to borrow, and sometimes even to copy, each other's prints. Most of the drawings of maize in the illustrated herbals studied here are reprints, and a few are copies. A survey was made of all of them to find the first plant of each original cut modelled after an actual maize plant. Since some of the cuts were reprinted for over 100 years, first prints were sought in order to date the depicted maize more accurately. Originals are more valuable than copies in such a morphological study as this, because, in the course of copying, the original figures might have been changed, either through misinterpretation or stylization.

In detecting reprints, like drawings were grouped together and then examined minutely to determine if similar prints had actually been made from the same block. Each print has a number of peculiarities, such as broken lines, which were compared in suspected duplicates. Some reprints had to be traced through as many as ten herbals extending over a century.

Each of these first [93] prints was then compared to determine if any were copies. The test for originality was not only distinctly different artistic features, but biological evidence that each print had been drawn from an actual maize plant as model. Some of this evidence is in the form of new biological features not found in previous cuts. For example, the cut in the 1566 edition of the herbal of Dodonaeus (fig. 8) presents among other original features "flag" leaves. The cut of l'Obel, in his edition of 1581 (fig. 9), shows prop-roots not found in earlier cuts. Evidence for originality is also presented when biological errors in previous cuts are not perpetuated. The husks in the large cut of Fuchs' herbal (fig. 4) are drawn in an unnatural position. Dodonaeus' cut (fig. 8), on the other hand, presents them life-like.

The woodcuts in the forty-seven illustrated herbals surveyed here were traced to originals in seven herbals. Only one cut had been copied extensively. The

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[92] Church, *op. cit.*, p. 233.

[93] The detection of a reprint where the original may be unknown is, of course, impossible. Therefore, some of the cuts which have been deemed "original" in this study may not have been original in the work to which they were traced, but may have been reprinted from previous herbals not in the collection of the Missouri Botanical Garden Library.

large cut in the first herbal of Fuchs, the first drawing of maize in the herbals, had such far-reaching influence that a number of cuts for the next hundred years were copied from it. This cut, of folio size, was probably considered too large for re-printing and was reduced in later herbals to 4¾ inches and to 2½ inches. (Since cuts were usually reduced by pantograph, they appear in reverse of the original. See Appendix I). Bock, in his herbal of 1546, presents an illustration of a stalk which is unquestionably a pantograph copy of one of the four stalks in the Fuchs herbal. The 1551 edition of the herbal of Lonicerus contains a cut of a plant with two stalks, taken from the Fuchs cut. Matthiolus, in his herbal of 1570, shows a plant that is very likely a stylization of the one in Fuchs (fig. 3). In addition, the herbal of Bauhin of 1651 gives a pantograph copy of three right stalks of a reduction of Fuchs' cut. A complete trace-list of all cuts in the herbals surveyed is found in Table IV.

All significant biological features were examined in these originals: the number of stalks, the number of ears borne on a stalk, the presence or absence of prop-roots and "flag" leaves, the shape of the ear, the number of rows of kernels, and, where possible, the arrangement of the tassel branching. A description of the cuts follows:

Fuchs, 1542:

Fuchs presents a culm bearing three tillers, two of which have one ear each (fig. 4). The culm bears four ears, the topmost being partially husked and showing eight regular rows of rounded kernels which taper toward the tip. This cut, of folio size, was reduced and used in thirteen later herbals. In the 1545 edition of Fuchs' herbal, the cut was reduced to 4¾ inches in length (fig. 5), but retained all gross features of the original. This reduced cut was also used in the editions of 1595 of the herbal of Fuchs, and of 1552, 1553, 1554, 1563, and 1578 of the herbal of Dodonaeus. The cuts in the editions of 1549, 1551, and 1553 of the herbal of Fuchs were reduced to 2½ inches (fig. 6).

Bock presents in his herbal of 1546 (fig. 7) a simplified copy of the cut in the Fuchs herbal of 1542,[94] which is used in later editions of his herbal (1552 and

[94] The single stalk in Bock's cut is a copy of the third stalk in the cut of Fuchs. Note that the arrangement of the leaves on both stalks is almost identical. (The cut was likely copied by pantograph, and hence all features are in reverse). On both stalks the top leaves are drawn opposite instead of the natural alternate arrangement, the third leaf from the top is incurved and has a small bract-like projection opposite it, and one of the basal leaves is bent around and in back of the stalk. Also, in proportion to the relative sizes, the leaves are drawn in both cuts at approximately the same internodal distance. Both stalks bear four ears. The Bock cut copies the Fuchs presentation of an ear with husks drawn only one-half way in an unnatural position, probably in order to expose the top half of the ear. In both cuts the corn silks are drawn extending from the tip of the ear, rather than from the kernels as actually occurs. The top two ears on both cuts are drawn from one node. Both stalks have ears of eight rows, but the third ear from the top on the Bock cut is husked one-half way, displaying a second ear of eight rows; this ear is covered in the Fuchs drawing. The husk arrangement of these two ears is very similar, however. The lowermost husk on both ears is drawn hanging down and around the lowest stalk. This indicates that Bock's artist possibly recopied the top ear in the third-ear position.

1560) and in the herbal of Valerius Cordus of 1561. Similar but somewhat stylized copies are found in the 1570 and 1583 editions of the herbal of Matthiolus; the 1651 edition of the herbal of Bauhin; the 1656 edition of the herbal of Pancovius; and the 1666 edition of the herbal of Chabraeus.

Dodonaeus, 1566:

The gross morphological features of the plant in the 1566 edition of Dodonaeus' herbal are completely different from those in Fuchs' cut (fig. 8). The tassel branches are firmer and more highly condensed, with a strong central spike. The ears are drawn with husks bearing distinct "flag" leaves—a feature only sketchily drawn in the cut of Fuchs. Inset is an ear of a higher row number than that in the Fuchs cut. The block of Dodonaeus is used in three later editions of the herbal (1583, 1616, 1644), in three editions of the herbal of l'Obel (1576, 1581, 1591), in one edition of Gerarde's herbal (1636), and in one herbal of Parkinson (1640).

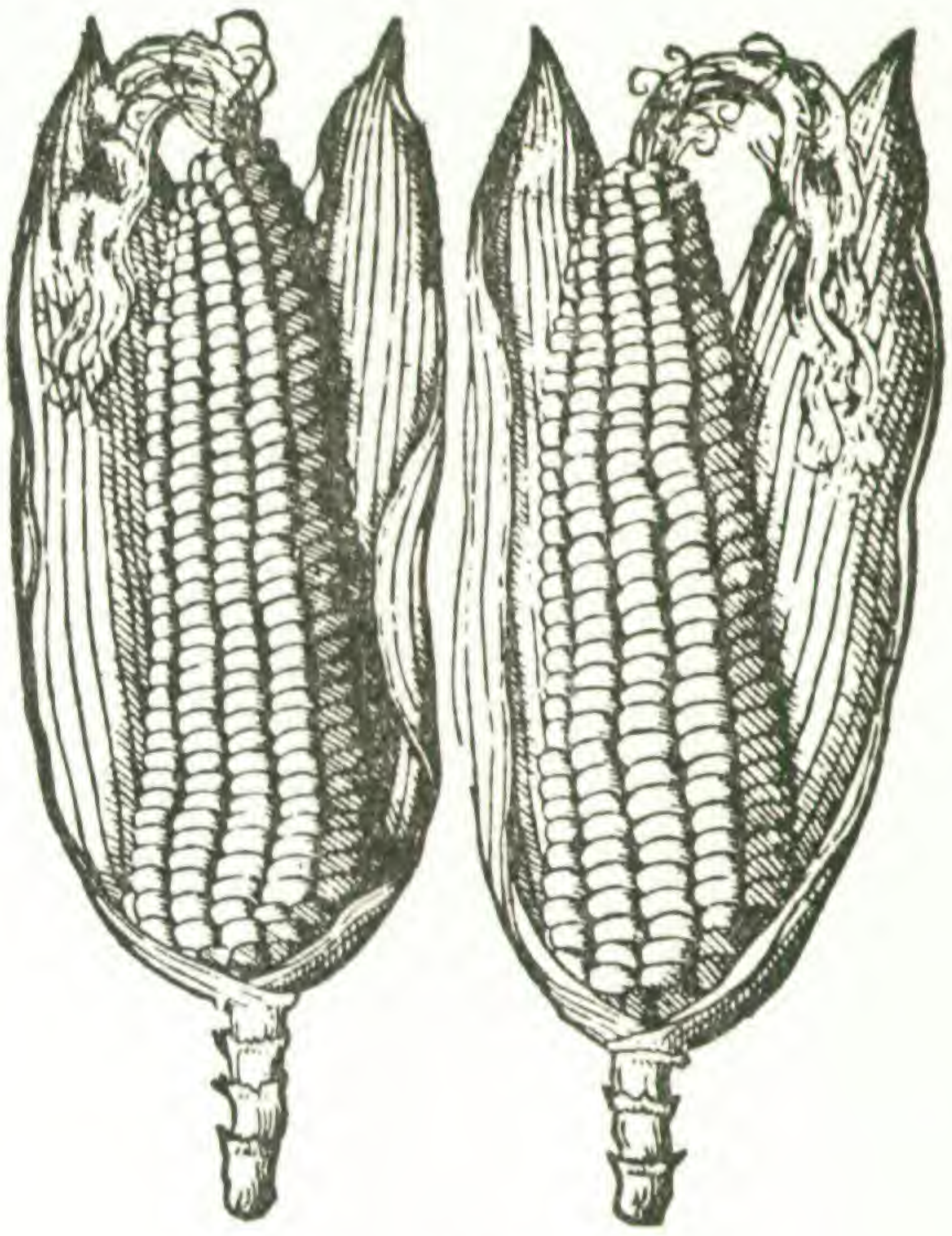
11

Fig. 11. "Turkish Corn" (Plant A) of Tabernaemontanus (1588). Note that the plant is without prop-roots.

12

Fig. 12. "Indian Corn" (Plant B) of Tabernaemontanus (1588). Note the very distinct "flag leaves" and prop-roots.

13



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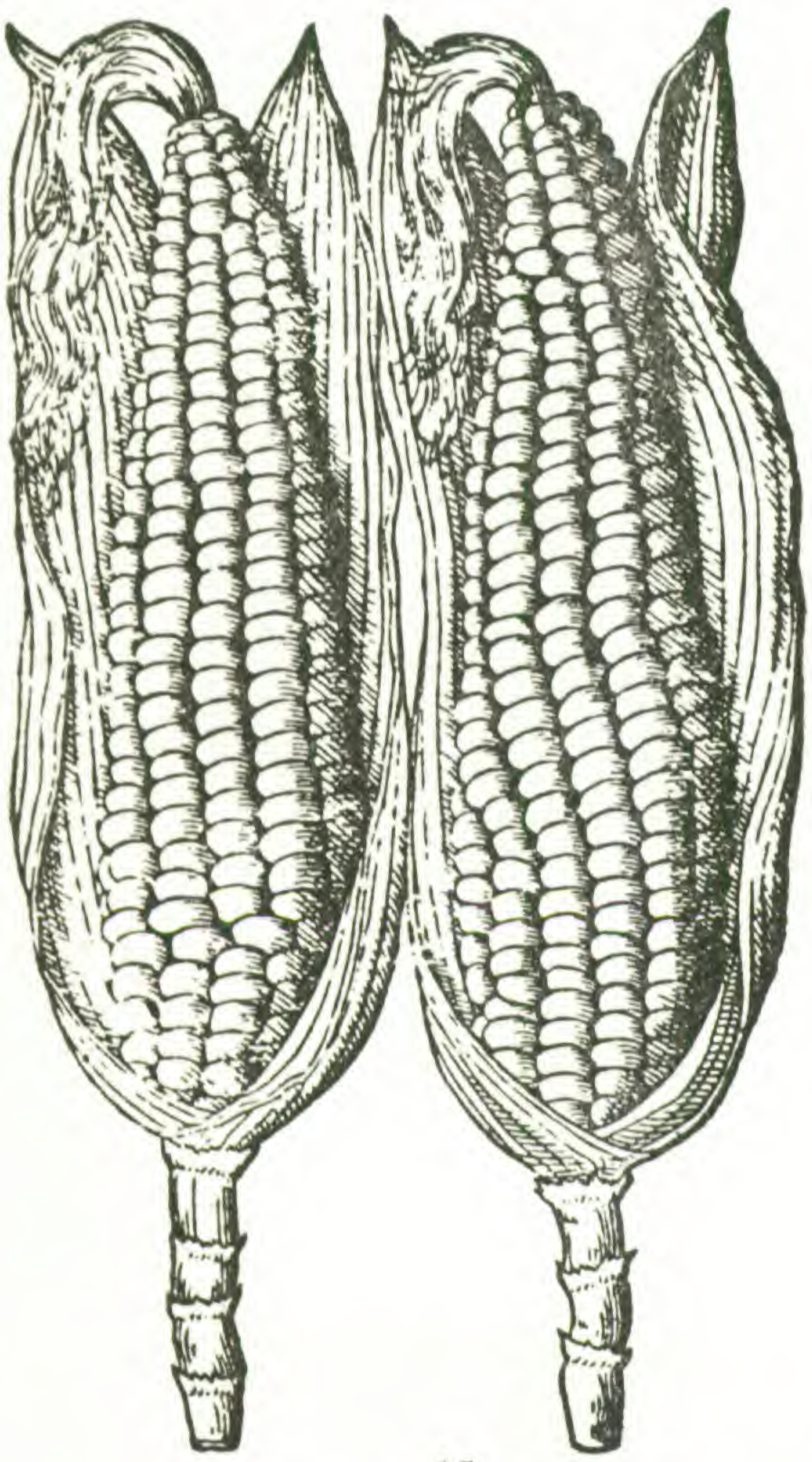

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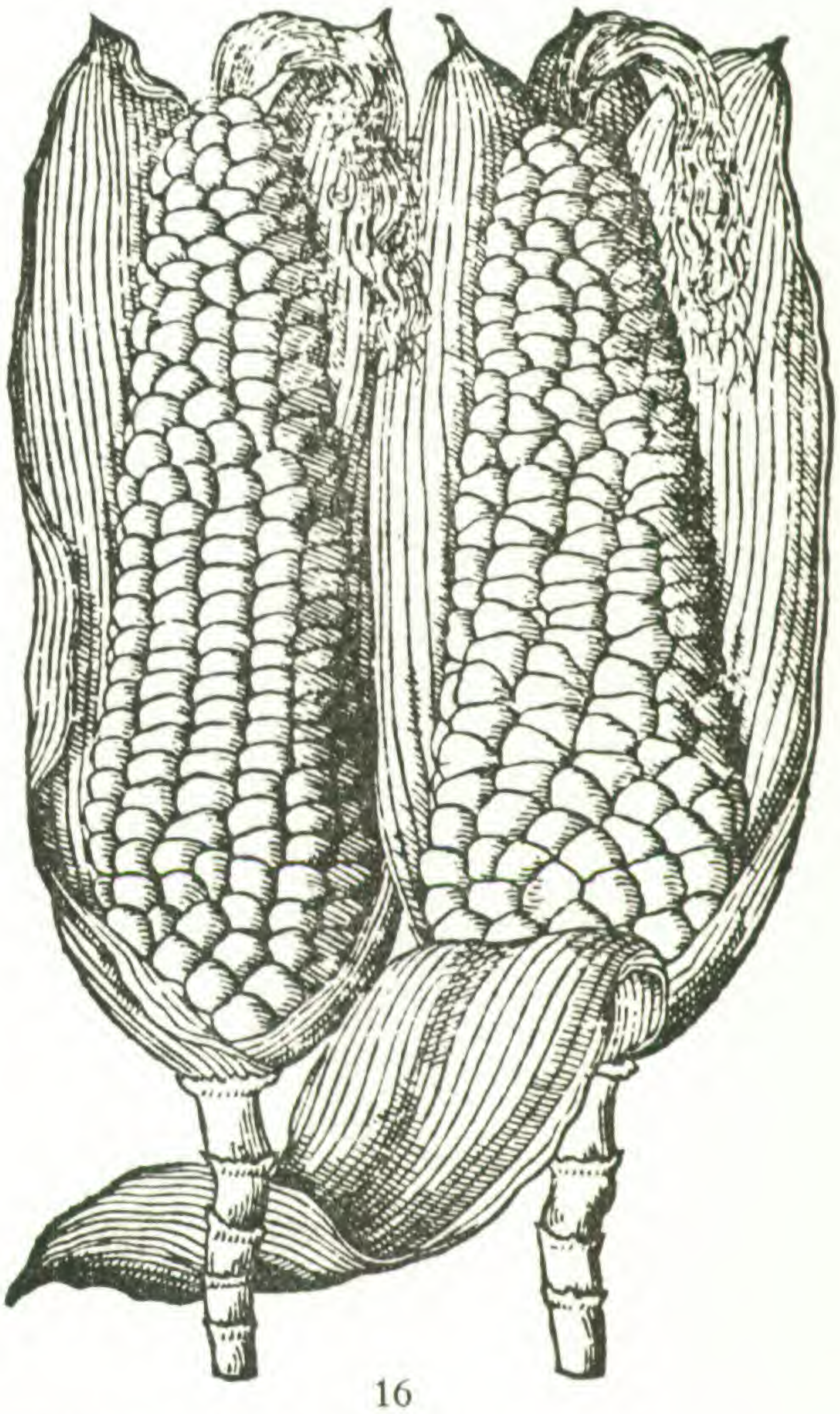

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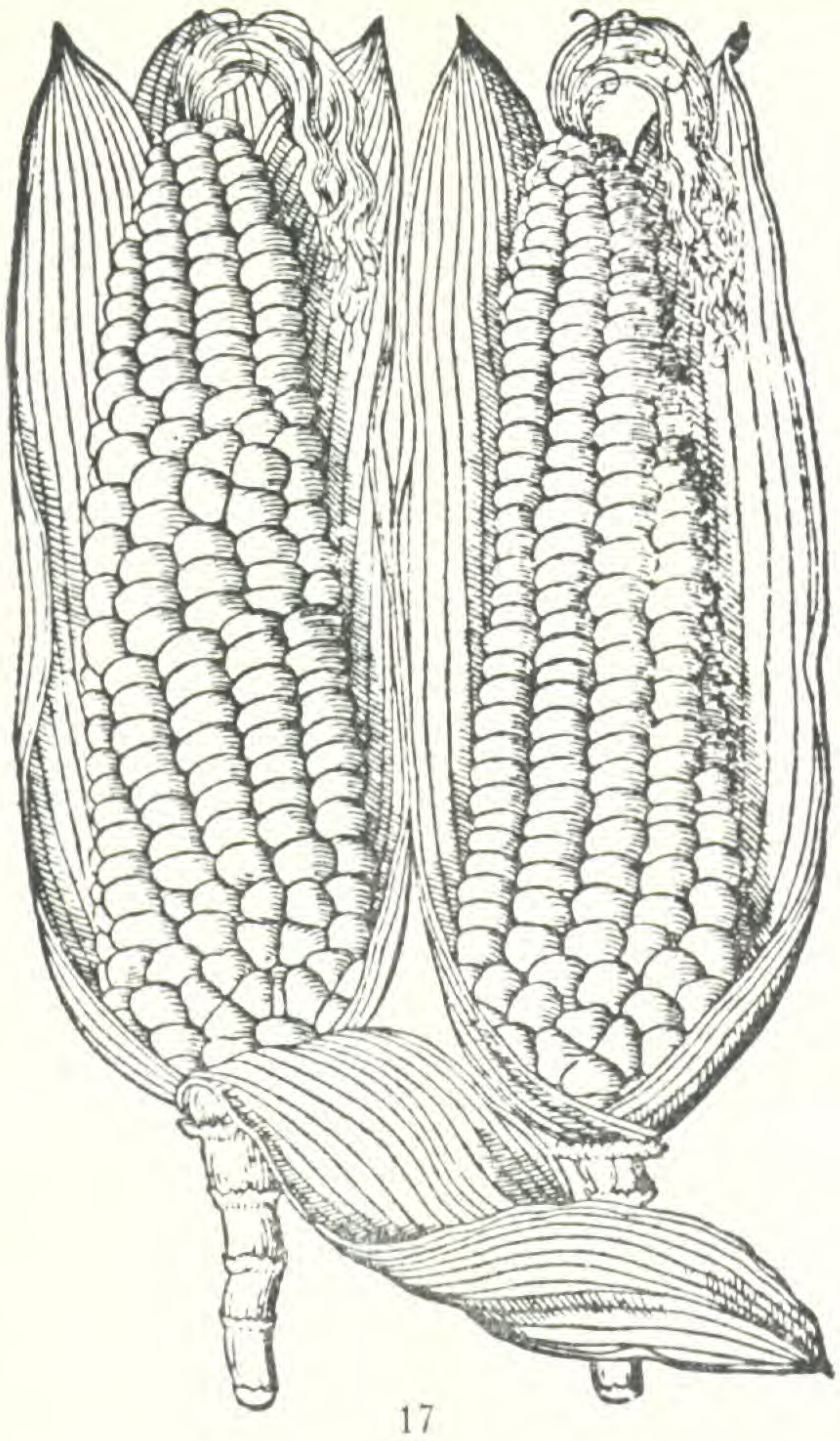
Figs. 13–16. Ears in the herbal of Tabernaemontonus (1588):

Fig. 13. "Red Turkish Corn" (left) and "Purple Turkish Corn" (right). Fig. 14. "Yellow Turkish Corn" (left) and "White Turkish Corn" (right). Fig. 15. "White, Brown and Dark Blue Indian Corn" (left) and "Speckled Indian Corn" (right). Fig. 16. "Red and Brown Indian Corn" (left) and "Yellow and White Indian Corn" (right).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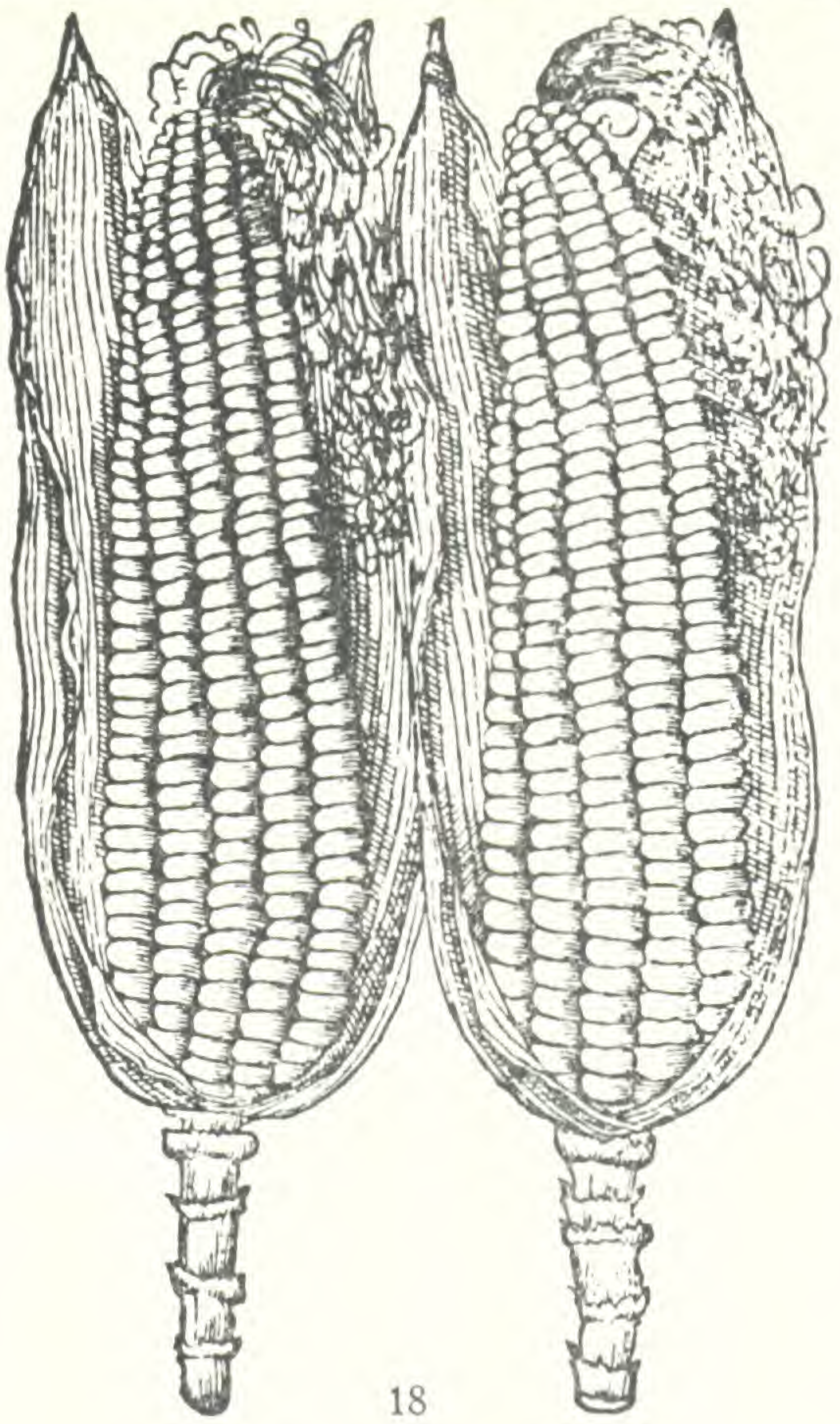
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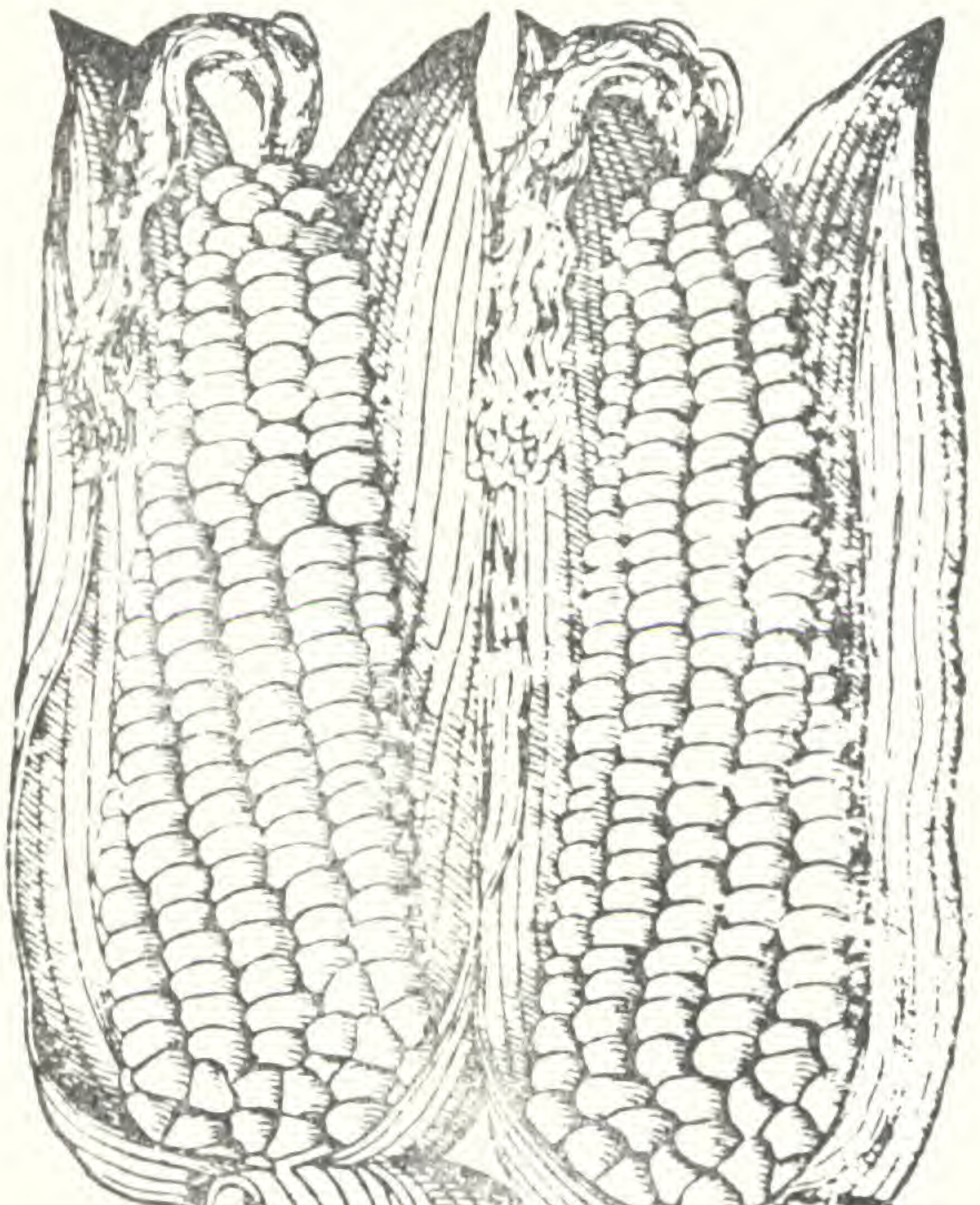
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Figs. 17–20. Ears in the Tabernaemontanus herbal (1588):

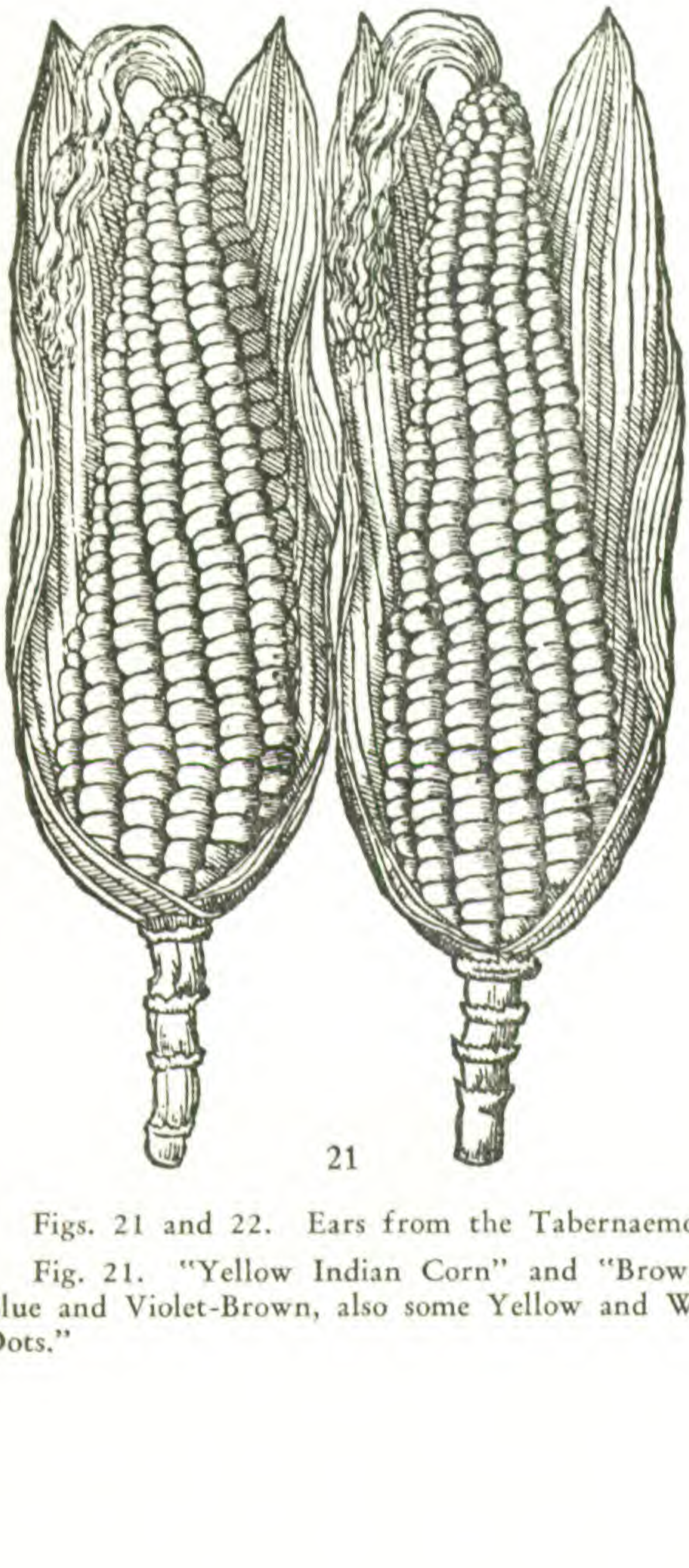
Fig. 17. "Violet-colored Indian Corn" (left) and "Golden Indian Corn" (right). Fig. 18. "White Indian Corn" (left) and "Black Indian Corn" (right). Fig. 19. "Red, Black and Brown Indian Corn" (left) and "White, Violet, Brown and Yellow sprinkled with Brown Dots" (right). Fig. 20. "Ears of Indian Corn."

l'Obel, 1581:

This was the first woodcut to present a stalk with prop-roots (fig. 9). These grow out at the lower nodes of the stalk in most varieties of maize and are conspicuously over-developed, as has been pointed out, when the plant is moved northward from the Tropics. Many features of the plant are highly stylized in this cut. The flag leaves are drawn with flourishes. The tassel branches are pictured as extending from the tip of the culm. The silks flow wavily from the ears. The stalk is bisected, probably in order to fit the whole plant into the cut. This is reproduced in a later edition of l'Obel's herbal (1591), in the herbal of Gerarde (1636), and in that of Hernández (1651).

Camerarius, 1586:

This cut (fig. 10) portrays a dwarfed plant, with an ear showing silks growing out from the kernels, an enlarged tassel branch, and an enlarged spikelet. The ear is of about eight rows. Freak plants were generally looked upon as portents during this period and for this reason they were frequently included in the herbals, even though they were not representative of their type. This cut is reproduced in the 1586, 1611 and 1678 editions of the herbal of Matthiolus and in the 1609 edition of the herbal of Durante.



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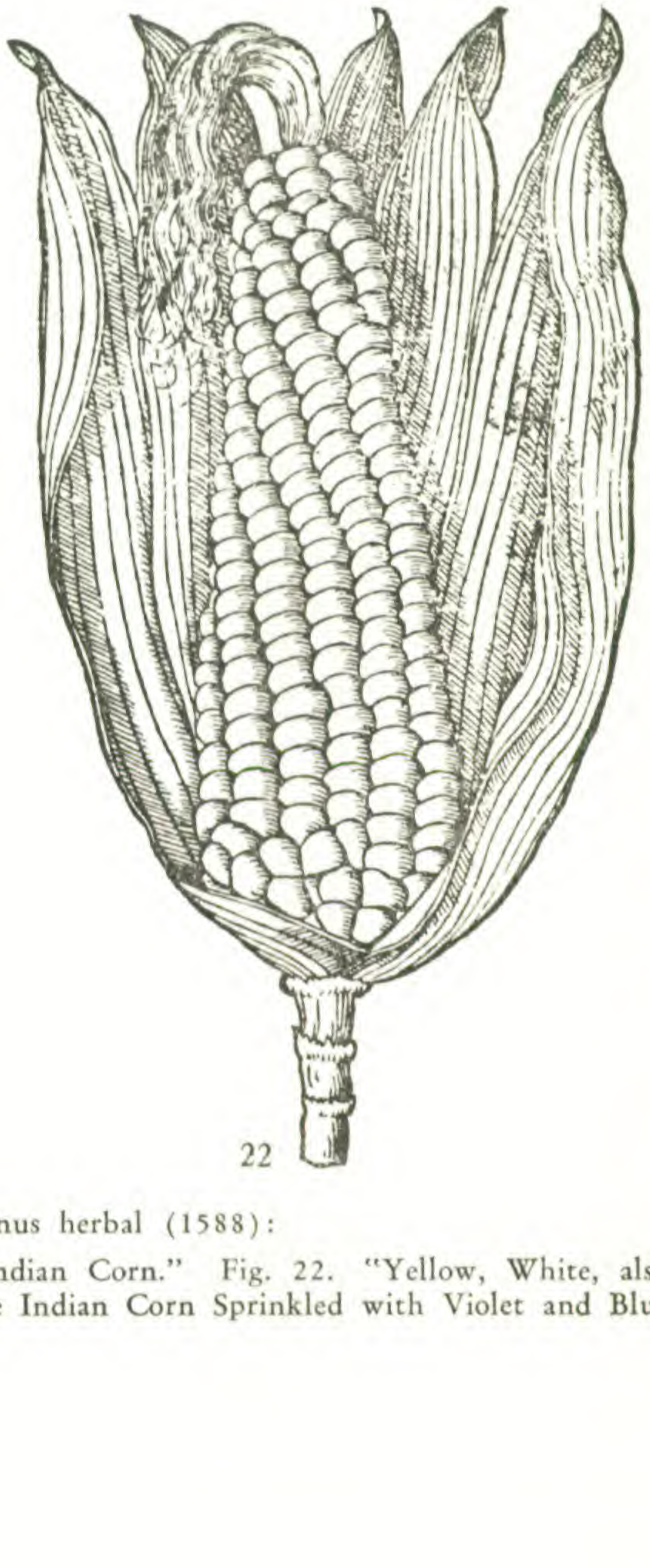

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Figs. 21 and 22. Ears from the Tabernaemontanus herbal (1588):

Fig. 21. "Yellow Indian Corn" and "Brown Indian Corn." Fig. 22. "Yellow, White, also Blue and Violet-Brown, also some Yellow and White Indian Corn Sprinkled with Violet and Blue Dots."

Tabernaemontanus, 1588:

The 1588 edition of the herbal of Tabernaemontanus presents two stalks of maize and 21 ears. One plant (A) (fig. 11), labeled *Frumentum Turcicum*, has three very slim ears without "flag" leaves, has highly condensed tassel branches and no prop-roots. The second plant (B) (fig. 12), named *Frumentum Indicum*, bears three very fat ears, a higher number of tassel branches, and three rows of prop-roots. This plant differs from that portrayed in the l'Obel cut (fig. 9) in its firmer, more natural tassel branches, less artistic flourishes in the corn silks and "flag" leaves, and having fewer rows of prop-roots. Four realistic ears (figs. 13 and 14) are presented under the heading *Frumentum Turcicum* and seventeen (figs. 15–23) under the heading *Frumentum Indicum*. The names for these cuts are reversed in later editions of Tabernaemontanus and in copies in other herbals.

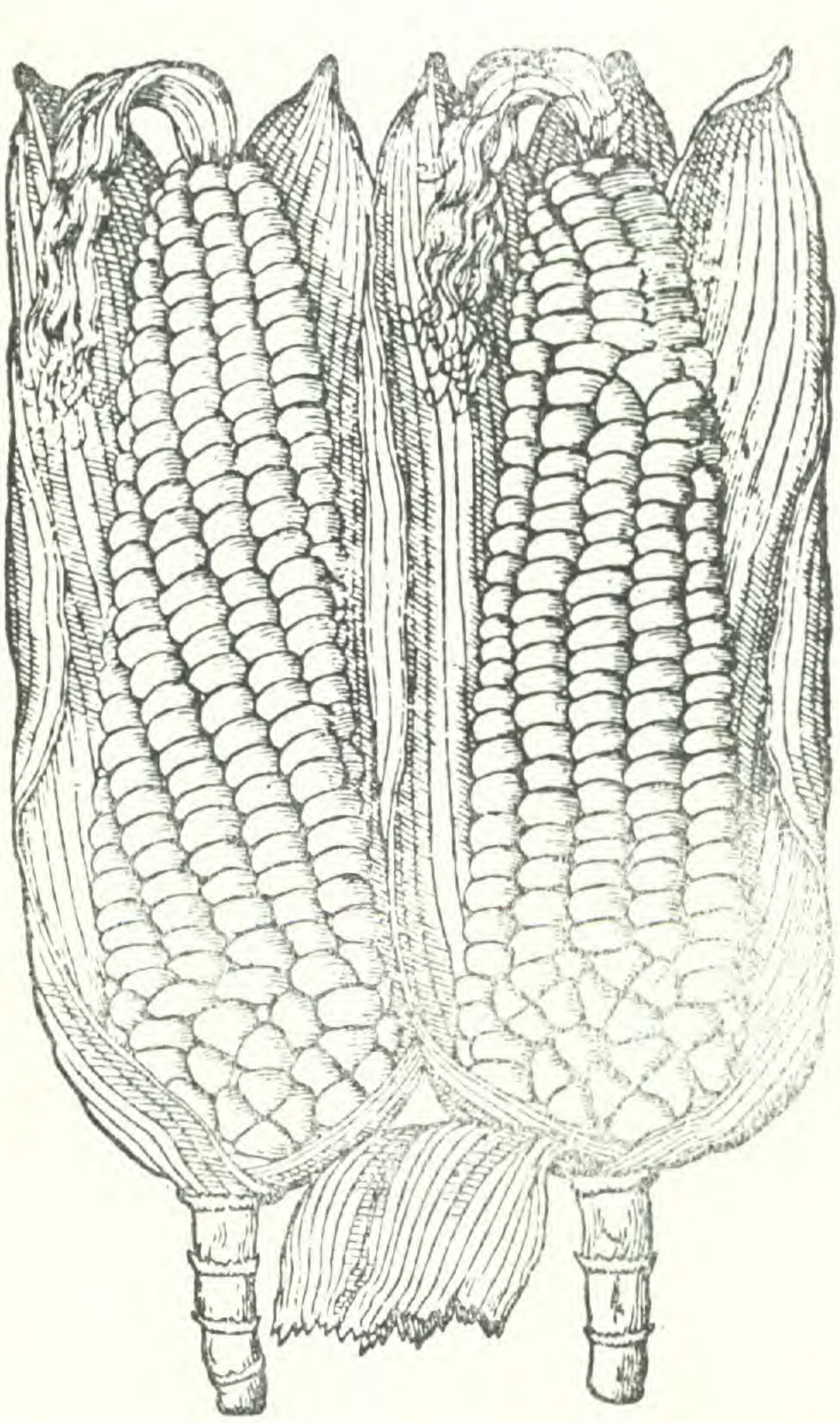

Fig. 23. "Dark Blue, Yellow, White and Speckled with Dark Blue Dots," from Tabernaemontanus (1588).

The cut of Plant A is reproduced in the later herbals of Tabernaemontanus of 1613 and 1664 as *Frumentum Indicum* and in the herbal of Bassaeus of 1590. The cut of Plant B is reproduced in the Tabernaemontanus herbals of 1613 and 1664 as *Frumentum Turcicum*, in the Bassaeus herbal of 1590, and in the herbals of Matthiolus of 1674 and 1698. All the ears are reproduced in the later editions of the herbal of Tabernaemontanus.

Bauhin, 1651:

Bauhin presents a drawing of an ear of about ten rows with silks drawn realistically. Inset are several types of enlarged kernels: long and flat; round and pointed; round and unpointed. (See fig. 24.)

Boccone, 1674:

In his edition of 1674, Boccone shows a freak plant with both the male and female inflorescences growing out from one branch. Like the plant in Camerarius' edition of 1586, this freak was probably presented as a portent. (See fig. 25.)

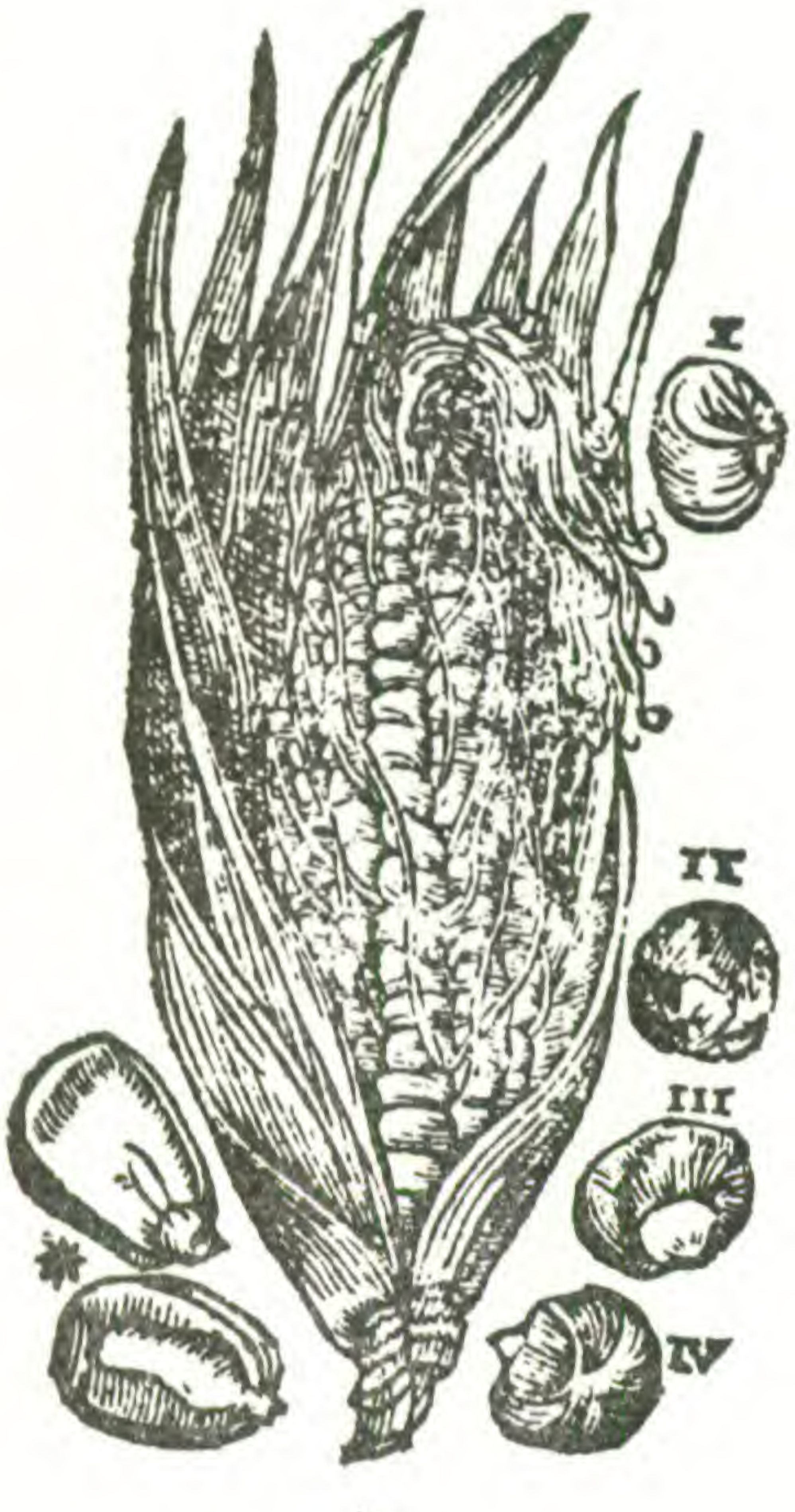

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Fig. 24. Illustration of an ear from the herbal of Jean Bauhin (1651), showing enlarged kernels of several types.

25

Fig. 25. A freak maize plant (Boccone, 1674), with both the male and female inflorescences growing out from one branch.

TABLE IV

WOODCUTS OF MAIZE IN THE 16TH AND 17TH CENTURY HERBALS

Herbals containing original woodcuts of maize	Reprints	Reductions	Copies
Fuchs, 1542	None	Fuchs, 1545 Fuchs, 1549 Fuchs, 1549 (Fr.) Fuchs, 1551 Lonicerus, 1551 Dodonaeus, 1552 Fuchs, 1553 Dodonaeus, 1553 Dodonaeus, 1554 Dodonaeus, 1563 Dodonaeus, 1578 Dodonaeus, 1578 (Eng.) Fuchs, 1595	Bock, 1546 Bock, 1552 Bock, 1560 Cordus, 1561 Matthiolus, 1570 Matthiolus, 1583 Bauhin, 1651 Pancovius, 1656 Chabraeus, 1666
Dodonaeus, 1566	L'Obel, 1576 L'Obel, 1581 L'Obel, 1591 Dodonaeus, 1583 Dodonaeus, 1616 Gerarde, 1636 Parkinson, 1640 Dodonaeus, 1676		
L'Obel, 1581	L'Obel, 1591 Gerarde, 1636		Hernández, 1651
Camerarius, 1586	Matthiolus, 1586 Durante, 1609 Matthiolus, 1611 Matthiolus, 1678		
Tabernaemontanus, 1588* (Plant A)	Bassaeus, 1590 Gerarde, 1597 Tabernaemontanus, 1613 Tabernaemontanus, 1674		
Tabernaemontanus, 1588 (Plant B)	Bassaeus, 1590 Gerarde, 1597 Tabernaemontanus, 1613 Tabernaemontanus, 1664 Matthiolus, 1674 Matthiolus, 1678		
Bauhin, 1651	Chabraeus, 1666		
Boccone, 1674			

* Tabernaemontanus presents cuts of 21 ears along with the stalk illustrations. One or two of these are sometimes reproduced, as in the herbal of Gerarde, 1636.

Conclusions

In the literature of exploration, the descriptions of maize are mostly fragmentary and inexact; in the herbals they are generally precise and well illustrated. Although we are now in a position to discuss authoritatively the maize of the herbalists, much more research will be necessary before we can speak with equal authority on the maize of the New World in early post-Columbian times. The literature of exploration is so vast, and bibliographic aids for consulting it are still so few, that it will take years of work to bring the data together for critical consideration. Some conclusions can already be drawn, however. We know that maize was widespread in the New World, was of a variety of types, and was used for various special purposes, such as in brewing, coloring food, for fat and oil, and in ceremonies. These indicate a relatively long use in the hands of skillful cultivators.

What do the herbals contribute to the history of maize? Their chief value is in enlarging our understanding of the types of maize in post-Discovery Europe. Our information in the herbals comes from two sources: text and illustrations. There is not always exact correlation between the two where both appear. As has been pointed out above, the herbalists frequently borrowed or copied each other's woodcuts, and this was done apparently without determining whether the material coincided with their text. Dodonaeus, for example, in his herbal of 1566, describes an ear of eight to ten rows; yet in his illustration he includes an ear which appears to have ten to twelve rows (see fig. 8). Both sources of information, therefore, have to be considered separately in determining their biological significance. Generally it is from the woodcuts, where such detailed items as kernel shape, presence of prop-roots, etc. can be observed, that we get most of our information.

How much of the text on maize is original in each of the herbals is hard to determine. The classical tradition of copying from previous works was especially true of the herbals. Their purpose, it must be remembered, was to allow the reader to associate the particular plants of his region with those medically efficacious plants described by the ancients. For example, in the herbal of Brunfels, the first of the German Renaissance fathers of botany, descriptions are taken verbatim from those of the ancients. With such a tradition, it is not unlikely that the herbalists might have copied from each other descriptions of new plants. A number of characteristics appear much the same in most of the descriptions of maize. Wherever the row number of the ear is mentioned in sixteenth-century herbals, an eight- to ten-rowed ear is described. The growing season likewise is generally the same—late March or April to late August or September. Some of the material, such as the discussion of maize in the herbal of 1570 of Matthiolus, was influenced by the New World chroniclers. The validity and originality of the woodcuts have been discussed above.

The material of most value—both from text and woodcuts—comes from herbals of the sixteenth century. Most of the woodcuts of the seventeenth century

herbals are reprints or copies (See Table IV), and the texts, for the most part, are similar to those of the preceding century. Moreover, in the later period, maize was probably being reintroduced at various times and from various places and the original introductions were probably hybridized.

The information presented here cannot be classified definitively. A comprehensive classification of maize is not yet in existence (see Anderson and Cutler, 1945). For some time to come, a complete and natural classification of the maize of the world must be a project to work toward. Enough has already been done, however, to point to certain significant characters of the corn plant which will help us determine the inter-relationships of various types. From studies of the maize of Mexico (Anderson, '46), of the United States Southwest (Carter and Anderson, '45) and the Northeast (Brown and Anderson, '47), and of Central America (Anderson, '47) it has been learned that the following characteristics are particularly important in tracing the racial history of maize: row number; breadth of culm; number of tassel branches; kernel size and shape (whether pointed or dented); ear shape; leaf width; absence or presence of "flag" leaves, and of prop-roots. With these characteristics in mind, it is clear that there are at least two distinct types of maize discussed in the herbals. In the later herbals, where both types appear, they are distinguished by different names. The first type, that described and illustrated by Fuchs (1542, fig. 4), Dodonaeus (1566, fig. 8), and Tabernaemontanus (*Frumentum Turcicum*, 1588, fig. 11), is without prop-roots. It has an ear of about eight to ten rows, with some "flag" leaves, few tassel branches, and a generally slender culm. These characteristics are similar to those of Northern Flints—a type of maize recently studied and described by Brown and Anderson ('47, p. 2):

> The ears of the northeastern flints are characteristically long and slender with 8–10 rows of wide, crescent-shaped kernels . . . There are usually very few prop-roots above the levél of the soil surface. The culms are small and slender with long internodes and are lighter green than most dent varieties. The leaves are narrow and the ears are borne on long shanks. The leaves of the ear shoot (the husks) have conspicuous blades which are sometimes referred to as "flag leaves" by sweet-corn breeders.

The ear in the Fuchs illustration is clearly eight- to ten-rowed—a character also mentioned by Fuchs in his text. The ears described and illustrated by Tabernaemontanus (1588, figs. 13–23) also number about ten rows. The ear in the Dodonaeus woodcut, however, which is inserted without husks at the bottom of the drawing, appears to have a somewhat higher row number (about 12 rows), although in the text he describes it as having eight to ten rows. This ear, strongly tapering and perhaps of the dent type, might very well have been drawn from a different plant from that used as model for the cut. The kernels in the illustrations of Fuchs and Tabernaemontanus are distinctly rounded like flint kernels.

Certainly the most interesting characteristic of this first type of corn is its lack of prop-roots. These develop conspicuously when many (although not all) tropical varieties are moved farther north. The lack of them in all the early plates and in most of the descriptions leads us to wonder if the corn first described

by the herbalists was that introduced from the Caribbean by the Hispanic explorers. These plates and descriptions indicate a type of corn other than those whch might most readily have come from the tropical regions of the Caribbean. Both l'Obel (1581) and Tabernaemontanus (1588) present illustrations of this type of maize without prop-roots and distinguish it from another type (discussed below) containing several rows of roots. They label the former *Frumentum Turcicum* (Turkish Corn), and the latter, *Frumentum Indicum* (Indian Corn). Parkinson (1640) points out explicitly that the plant without prop-roots was prevalent in England and that the plant with such roots was a "stranger". Flag leaves, another characteristic of flint corns, are especially noticeable on the plant of Dodonaeus. They are not shown, however, in Fuchs' illustration (where the husks are drawn unnaturally) nor in the *Turcicum* cut of Tabernaemontanus. The other characteristics, a slender culm and a few branches, can only be approximately studied from the illustrations.

At the present time we can only speculate on what type of maize this is. It might have been a Northern Flint, having, as has been pointed out, a number of outstanding similarities. Such speculation naturally starts further questioning as to where this type of maize originated and how it was introduced into Europe. We know from the material in the herbals that it was grown in Germany and the Low Countries at least fifty years after the Discovery of America. The herbalists generally claimed that it came from the Orient. Fuchs (1542) says it was brought into Germany from Greece or Asia. Dodonaeus, in early editions, calls the plant *Milium Indicum* and associates it with the plant of Pliny, but in his edition of 1566, where his own drawing is first presented, he concludes that the plant is unlike anything described by the ancients. Tabernaemontanus expressly distinguishes this type, which he labels *Frumentum Turcicum*, from another which he calls *Frumentum Indicum* and which he says was brought in from the New World. He makes no mention of the possible origin of the *Turcicum* plant but from the name he very likely assumed an Oriental origin.

How a Northern Flint type might have reached Europe at such an early date can only be guessed. It is known that the Northern Flints described by Brown and Anderson were widespread in eastern North America in pre-Columbian times. According to legend, two Norsemen, Karlsefn and Thorfin, in the years 1002 and 1006 A.D., brought back ears of corn to Europe from what is now Massachusetts (Bowman, '15, p. 1). Could this be the maize that found its way in the gardens of the herbalists? Or could it have been from a plant possibly brought into Europe during the first quarter-century after the Discovery by some English explorers—especially since Parkinson (1640) reports that the corn without prop-roots was most prevalent in England? If not, then it might be some variety, as yet unstudied, from the Caribbean, without the conspicuous characteristic of prop-roots. Such varieties have recently been discovered in the Amazon basin by Cutler, but as yet these types have not been reported from the Caribbean. Maize from this area was very probably introduced by many of the Hispanic explorers or even

by Columbus himself. It could easily have reached Germany from Spain quite early as both were part of the empire of Charles V and there was extensive trading between the two countries.

The second type of maize, illustrated by l'Obel (1581, fig. 9) and by Tabernaemontanus (1588, fig. 12), seems to be one of the common corns from the Caribbean area. It has a number of similarities to maize of this tropical region. As usually occurs when these plants are moved out of the tropical zone north into the temperate zone, several rows of prop-roots sprout from the lower nodes. The ears depicted by Tabernaemontanus tend to be higher-rowed, another characteristic of these corns. Both l'Obel and Tabernaemontanus make a distinction in their illustrations between this type and that described above. This type is labeled in both herbals "Indian Corn," and its origin, according to Tabernaemontanus, is America. L'Obel, on the other hand, believed that it was similar to the plant described by Pliny. Such a maize was very probably introduced into Europe by the Hispanic explorers and reached Germany by the routes discussed above.

Summary

We now know that two general types of maize are discussed in the herbals. The first type, which was first illustrated fifty years after the discovery of America (Fuchs, 1542), is similar to the typical flints of eastern North America and was believed by most of the herbalists who discussed it to have been brought into Europe from Asia. Where such a type of corn actually came from can only be speculated upon. It may be some as-yet-unknown tropical variety closely related to our flints, but the final answer will have to await further study. The second type of maize, recognized by herbalists in the latter half of the sixteenth century as different from the first and reported by them to have been brought in from America, is much like the present-day corn of the Caribbean area and was very likely introduced into Europe by the early Hispanic explorers.

Appendix I

THE WOODCUTS OF THE GREAT HERBALS

All of the illustrations in the herbals were printed from wood blocks. A knowledge of how woodcuts are made, how they differ from other graphic processes, and how they can be copied is helpful in understanding much of the data on maize in the herbals.

Historical Background of Woodcuts.—

As early as 1041, woodcuts were used by the Chinese to illustrate books. In Europe before the discovery of the printing press, there was a wide use of block-books in which both text and illustrations were printed from woodcuts.[95] In the century after the discovery of the printing press, woodcuts found their widest use and attained the peak of their artistic development as decorations and illustrations of the printed text. Woodcuts produce prints from an inked surface in relief, as does type. Both the cut and the type could be inked at the same time and, where desired, both could be used on the same page. Intaglio printing, on the other hand, which is not in relief, requires a separate inking and cannot be produced on the same page with the printed text.

How Woodcuts Are Made.—

In making a woodcut, the cutter worked from a design which was drawn, traced, or pasted directly on the wood block, generally about ⅞ inch thick. The parts of the block surface which were to print white were cut away, leaving the parts to print black in relief.[96]

There are two general types of woodcuts: the black-line and the white-line. All of the woodcut illustrations in the herbals are of the black-line type. The relief of the black-line cut is intended for the design itself, printing a black-line drawing against a white ground. In making this type of cut, the cutter merely cuts away from lines of a design drawn or pasted on the wood block. In the early period of the craft this work was often done by woodcutters who belonged to the class of the carpenter rather than to that of the artist.[97]

How Woodcuts Differ from Other Graphic Processes.—

Woodcuts differ from other illustrations in that the part of the block that is inked for printing is in relief. In intaglio engravings and etchings, on the other hand, the part inked for printing is cut into the surface. In lithography the printing is from the surface without relief or indentation.

Lithography was not known during the 16th and 17th centuries, so the woodcuts of this period have chiefly to be distinguished from metal relief cuts and intaglio-line engravings. Prints from the few metal relief cuts can be detected sometimes by the outline of the nails which fastened the metal plate on the wood

[95] Hind, Arthur M., *History of woodcuts,* pp. 35, 65–66.
[96] *Ibid.,* p. 7.
[97] *Ibid.,* p. 30.

block.[98] Prints made from woodcuts are impressed in the paper surface and in this way can generally be distinguished from intaglio prints which are raised slightly above the surface. A print from a woodcut does not show an outline of the boundaries of the block, as does that from an intaglio plate. The woodcut line is generally broader and less regular than the engraved line. Each side of the woodcut line has to be cut separately, but the engraved line is made by a single push of the burin and can be drawn very fine. The engraved line always ends in a point, while the woodcut line can be made either blunt or pointed at the ends, depending on the style of the artist.

Botanical Woodcuts.—

Botanical illustration, although gaining its greatest impetus from the woodcut, certainly did not begin with that graphic technique. Hand-painted illustrations of plants were used very early. Pliny reports that the herbal of Krateuas, who lived around 120 B.C., contained colored pictures of plants.[99] The famous Anicia Juliana Codex of Dioscorides (512 A.D.), which is still in existence, is similarly illustrated.[100] In fact, the early herbals were generally illustrated in this manner. Drawings such as these, copied and recopied throughout the Middle Ages, served as models for the first botanical woodcuts. The earliest book of this kind, *Das puch der natur* (The Book of Nature) of Konrad von Megenberg, printed in 1475, had been compiled three centuries earlier. The work had been widely copied before it was printed, since 35 manuscripts still exist.[101] The *Herbarum* of Apuleius Platonicus, which was published with illustrations in 1481, also had been copied and recopied for a long time, its possible origin dating as far back as the fifth century.[102] With each copying, the illustrations in these early herbals withdraw farther and farther from nature. The first botanical woodcuts, as a result, are little more than diagrams of the general appearance of plants and are often unrecognizable. Exact details of the plant, such as type of venation or peculiarities of leaf shape, are omitted.

The renaissance of botanical illustration started with the publication of Brunfels' *Herbarum vivae eicones* in 1530. The work is significant because its 135 woodcut illustrations were designed from actual plants. It was one of the first works to present pictures which even now retain their value as accurate scientific documents. Brunfels wrote at the beginning of his work:

> I have no other end than that of giving a prop to fallen botany; to bring back to life a science almost extinct. And because this has seemed to me to be in no other way possible than by thrusting aside all the old herbals, and publishing new and really life-like engravings, and along with them accurate descriptions extracted from ancient and trustworthy authors, I have attempted both . . .[103]

The realistic drawings in the work are important because they depict plants

[98] Ivins, *How prints look.* New York, 1943, p. 39.
[99] Arber, *op. cit.*, p. 8.
[100] *Ibid.*, p. 9.
[101] *Ibid.*, p. 14.
[102] *Ibid.*, p. 15.
[103] Greene, *op. cit.*, p. 172, as quoted from Brunfels.

whose morphology and anatomy were little known at the time the herbal was compiled. Little could be said about botany by earlier herbalists because little was known. Little could be described because few words had been created to describe botanical organs. The descriptions that were used had been copied mostly from the works of Greek and Roman writers handed down for more than 1000 years. Yet by means of realistic depiction, Brunfels was able to project the first important botanical message of the renaissance. And through use of the woodcut, the message was circulated widely—not only among physicians but also among students of the gradually developing new science of botany. The descriptions that could not be expressed in words were communicated in a more graphic fashion—a depiction in detail of the actual plant itself.

The realistic depiction of plants was continued on a larger and more elaborate scale in the herbal of Fuchs, *De historia stirpium* (1542). Of folio size, this edition contains 500 drawings 13 x 8 inches. Fuchs' herbal is especially significant in this study because it contains the first illustration of maize to be found in the herbals and among the first drawings of the plant to be published in Europe.

Copying Woodcuts.—

In a period when illustrations were expensive and plant models for woodcuts sometimes hard to get, woodcuts were frequently copied or borrowed by one herbalist from another. Copying a cut of the same size entailed merely tracing the design through transparent paper and pasting the paper on the block for cutting. Cuts were commonly reduced or enlarged by means of a pantograph—a device with a pen at each end, one being used to trace the design to be copied, the other attached to a hinged mechanism. This mechanical arm could be extended for reducing and closed for enlarging—copying the tracing mechanically in reverse of the original.

Many of the large cuts in Fuchs' herbal of 1542 were reduced by pantograph in later editions and published in reverse of the original. Other reductions, however, which had the design printed in the same position as in the original, were made by turning over the paper on which the design was pantographed before pasting it on the cut.

Appendix II

PASSAGES FROM ORIGINAL TEXTS QUOTED AND TRANSLATED

The following passages are the original text of the footnotes so numbered:

[10]Este pa*n* tiene la caña e asta en que nace ta*n* gruessa como una asta de una lança gineta: y alguna como el dedo pulgar e algo mas e menos segu*n* la bo*n*dad dela tierra do se siembra. E crece comu*n*mente mucho mas q*ue* la estatura de un ho*m*bre: e la hoja es como de cana comu*n* de Castilla: y es mucho mas lue*n*ga e mas a*n*cha e mas domable y mas verde e menos aspera. E cada una caña echa a lo menos una maçorca: e algu*n*as dos e tres: e ay en cada maçorca cc e a un.o. (sic ?) e mas y menos granos segu*n* la gra*n*deza dela maçorca. E cada maçorca esta embuelta en tres o q*ua*tro hojas o cascaras ju*n*tas e justas al grano unas sobre otras algo asperas: e q*ue*si de la tez o ge*n*ero de las hojas de la caña en q*ue* nace: y esta ta*n* guardado el grano por aq*ue*llas cortezas o cascaras que lo cubren . . .

[11]Como soy amigo de la leçion de Plinio, diré aqui lo que diçe del mijo de la India, y pienso yo que es lo mismo que en estas nuestras Indias llamamos mahiz, el qual auctor diçe aquestas palabras: "De diez años acá es venido mijo de la India, de color negro de grande grano: el tallo como cañas, cresçe siete piés: es dicho lobas é es fertilíssimo sobre todas las cevadas: de un grano nasçen tres sextarios: siémbrasse en lugares húmidos." Por estas señas que este auctor nos da, yo lo avria por mahiz, porque si diçe que es negro, por la mayor parte el mahiz de Tierra-Firme es morado escuro, ó colorado, é tambien hay blanco, é mucho dello amarillo. Podria ser que Plinio no lo vido de todas estas colores, sino de lo morado escuro que paresçe negro. El tallo que diçe que es como cañas, assi lo tiene el mahiz, y quien no lo conosçiesse e lo viesse en el campo, quando está alto, penssará que es un cañaveral. Los siete pies que diçe que cresçe, por la mayor parte acá es el mahiz algo mas alto, y tambien mucho mas, y en partes menos, segund la fertilidad ó bondad del terreno en que se siembra. Quanto á lo que diçe de ser fertilíssimo, ya he dicho lo que he visto, que es coger ochenta e çiento e çiento e cinquenta hanegas de una de sembradura: diçe que siembra en lugares húmidos: humidíssima tierra son estas Indias. Mas para comprobar la nescessidad que el mahiz tiene de estar puesto en tierra húmida, ó donde el agua le sea propiçia, digo que estando en Avila la Magestad de la Emperatriz, nuestra señora, á la saçon que el Emperador, nuestro señor, estaba en Alemania, vi en aquella cibdad, que es una de las mas frias de España, dentro de una casa, un buen pedaço de mahizal de diez palmos de alto las cañas, é algo mas é menos, é tan gruesas é verdes é hermosas, como se puede ver en estas partes, donde mejor se pueda haçer; y alli á par tenia una anoria de que cada dia le regaban. Y en verdad yo quedé maravillado, acordándome de la distançia y de los diferentes climas destas partes con Avila, y porque los testigos que diere desto, sean apropóssito mio, digo que en la misma casa possaba el muy reverendo señor doctor Bernal, del Consejo Real de Indias por Sus Magestades, é que agora es obispo de Calahorra, lo qual fué el año de mill é quinientos é treynta de la Natividad de Chripsto, nuestro Redemptor.

[11]*Pliny's original text:*

milium intra hos X annos ex India in Italiam invectum est nigrum colore, amplum grano, harundineum culmo. adolescit ad pedes altitudine VII, praegrandibus comis—iubas vocant—, omnium frugum fertilissimum. ex uno grano sextarii terni gignuntur. seri debet in umidis. (*Plini Secundi Naturalis Historiae Libri XXXVII*, Vol. III, Lipsiae, 1892, *Lib.* XVIII, *Cap.* 7, p. 157.)

The confusion between Oviedo's term *lobas* and Pliny's *iubas* was probably a textual misinterpretation.

[13]De un grano nasce una caña solamente; empero muchas veces una caña lleva dos y tres espigas, y una espiga cien granos y docientos, y aun cuatrocientos, y tal hay que seiscientos. Cresce la caña un estado y mas, engorda mucho, y echa las hojas como nuestras cañas; pero mas anchas, mas largas, mas verdes y mas blandas . . . Viene a sazón en cuatro meses, y en algunas tierras en tres, y a mas y medio en regadio, mas no es tan bueno.

[16]Tampoco tenían trigo en todas las Indias, que son otro mundo; falta grandísima segun la usanza de acá mas empero las naturales de aquellas partes no sintían ni sienten tal falta, comiendo pan de maiz, y cómenlo todos . . . Para comer pan cuecen el grano en agua, estrujan, muelen, y amásanlo; y, o lo cuecen en el rescoldo, envuelto en sus hojas, que no tienen hornos, o lo asan sobre las brasas; otros lo muelen el grano entre dos piedras como mostaza, ca no tienen molinos; pero es muy bien trabajo, asi por la dureza como por la continuación, que no se tiene como el pan de trigo; y así, las mujeres pasan trabajo en cocer cada dia; duro pierde el sabor y enderescese presto, y a tres dias se mohesce y aun pudre. Ensucia y daña mucho la dentadura, y por eso traen gran cuidado de alimpiarse los dientes.

[18] Todos por la mayor parte beben agua, pero á ninguno desplaçe el vino: antes son muy amigos dél, é aqueste haçen del mahiz, segund la cantidad que quieren haçer de *chicha*, que assi llaman á su vino, é para haçerlo tienen esta forma. Ponen el mahiz en remojo, é assi está hasta que allí en el aqua comiença a brotar por los peçones, é se hincha, é salen unos cogollicos por aquella parte quel grano estuvo pegado en la maçorca que se crió; é desque está assi saçonada, cuécenlo en buen agua, é despues que ha dada çiertos hervores é menguado la cantidad que ya ellos saben ques menester, apartan del fuego la olla ó tinajuela en que lo cueçen, é repóssase é assiéntase abaxo el grano. É aquel dia no está para beber: pero el segundo dia está mas asentado, é comiençan á beber dello, aunque está algo espesso: é al terçero dia está bueno é claro, porque está de todo punto assentado, y el quarto dia muy mejor, é la color dello es como la del vino coçido blanco de España, y es gentil brevage. El quinto dia se comiença a açedar, y el sexto más, y el séptimo es vinagre, é no para beberse . . .

[22] [los indios] beben tanta cantidad [del brebaje de maiz] que los emborracha; y para ese efecto se juntan en cuadrillas en casas particulares, haciendo unas danzas y bailes con atambres y instrumentos torpes; y es costumbre que nunca bebe ninguno destos indios esta bebida solo, sino que tienen todos los vasos a pares, y habiendo de beber el uno en uno de los dichos vasos, ha de dar de beber al compañero en el otro . . . .

[33] Aquel dia ú otro adelante de la fiesta . . . cogen muchos manojos de mahiz atados, é pónenlos alrededor del monton de los sacrifiçios é allí primero los maestros ó saçerdotes de Luçifer, que están en aquellos sus templos, é luego el caçique, é por órden los prinçipales de grado en grado, hasta que ninguno de los hombres queda, se sacrifican é sajan con unas navajuelas de pedernal agudas las lenguas é orejas y el miembro ó verga generativo (cada qual segund su devoçion), e hinchen de sangre aquel mahiz, é despues repártenlo de manera que alcançe á todos, por poco que les quepa, é cómenlo como por cosa muy bendita.

[53] Hoc frumentum, ut alia multa, ex eorum est genere quae aliunde ad nos translata sunt. E Graecia autem & Asia in Germania venit, unde Turcicum frumentum appellatum est: Asiam enim uniuersam hodie Immanissimus Turca occupat Germani etiam ad loca unde affertur respicientes, *Turckisch korn* nominant.

[56] Radicibus nititur multis, obliquis et fibratis, quibus etiam accedunt fulcra quaedam ab imo geniculo undique exeuntia, et in terram demissa, quibus vento agitata seges sustentatur . . .

[61] Hac aetate frumentum Turcicum, aut Saracenicum nominatur: inde quod ex Asia aut Graecia, quae Turcarum imperio modo parent, advectu*m* existimetur . . . . . .
. . . his ipsis frumentum Turcicum dissimile sit, non triticum Bactrianum, sed nouo tritici Turcici nomine potius nuncupandum, donec vetus eius nomen Oedipus aliquis demo*n*strarit, qui a veteribus alicubi descriptum, aut cognitum fuisse, persuadere queat.

[62] Haudquaquam ex Asia que Turcorum Imperatori paret, (ut a plurisque et vulgo creditum est) aut ex Oriente, sed ab Occidente et ex America, vicinisque insulis, in Hispaniam primum, deinde in alias Europae provincias invectum.

[66] Potest inter Tritici genera quoque recenseri illud frumenti genus, quod quidam perperam Turcicum appellant. Perperam, inquam, quod Indicum, non Turcicum, vocari debeat. Nam ex occidentalibus Indiis primo allatum est, non ex Turcia, et Asia, ut credidit Fuchsius.

Page 29.—

OVIEDO, 1535.

. . . ponense cinco o seys indios .. . uno desuiado del otro un passo en ala puestos y co*n* sendos palos o macanas en las manos y da*n* un golpe en tierra con aquel palo de punta e meneanle porque abra algo mas la tierra y sacan le luego. E en aquel agujero que hizo echan con la otra mano siniestra quatro o cinco granos de Mahiz que saca de una taleguilla que lleva ceñida o al cuello e con el pie cierra el hoyo con los granos porque los Papagayos e otras aves no los coman. E luego dan otro passo adelante e haze lo mesmo y desta forma a compas y prossiguiendo de un tenor: en ala todos aquellos indios siembran hasta que llegan al cabo dela haça o tierra que siembran e dela misma guisa bueluen al contrario e dan la buelta sembra*n*do hasta que hinchen toda la haça e la acaban de sembrar . . . (folios 71–72).

MATTHIOLUS, 1570.

Serunt Indi hoc semen, quod Malitz voca*nt*, hoc modo. Descendunt in agrum aliquot simul, recta linea dispositi, aequaliterque distantes, et deinde acuto palo terram perforant dextra manu et statim quatuor quin queve grana sinistra manu in unum quodque; foramen conjiciunt, pede altero foramenta occludentes, ne Psitaci semen depascantur. Et ita seriatim passu suo distantias metientes, agrum totum semine replent retrocedentes. Verum anteaquam semen terrae credant, biduo id aqua macerant, nec serunt, nisi prius terra pluvia maduerit. Nascitur infra paucos dies, e quarto in India demetitur mense (p. 305.)

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CONTRIBUTIONS TO OUR KNOWLEDGE OF AMERICAN CARBONIFEROUS FLORAS

X. An Osmundaceous Stem from Iowa[1]

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AND ROBERT W. BAXTER

Somewhat over a year ago we received from Dr. L. R. Wilson a collection of coal balls which had been obtained from the coal mine of the What Cheer Clay Products Co., What Cheer, Iowa. The petrifactions contain some especially well-preserved plant remains, among them undescribed Pteridosperm stems, lycopod leaves, and other fossils that will be dealt with in future contributions. The subject of the present account is a fragment of a small stem which we believe to be a very early member of the Osmundaceae. Although the central part of the specimen is well preserved the outer cortical tissues, as well as the great cloak of petiole bases, so characteristic of the family, are missing. While this renders impossible a comparison with a few fossil genera known only from outer cortical tissue and petiole bases (*Bathypteris rhomboidea* and *Anomorrhoea Fischeri*, in Kidston and Gwynne-Vaughan, 1909), it does appear to represent a significant link in our knowledge of the family, or the complex from which it originated. Moreover, a rather careful search through the collection has failed to reveal additional specimens, and since the mine has been abandoned our only course seems to be to record such evidence as is available.

Kidston and Gwynne-Vaughan presented in a series of four papers (1907-10) a monographic treatment of the petrified stem remains of plants referred to the Osmundaceae. These fossils are from widely scattered localities and range in time from the Miocene down to upper Permian horizons. The specimen described herewith is believed to be sufficiently distinct to be designated as a new genus, and if our concepts of its relationships to the fossils of Kidston and Gwynne-Vaughan be correct it extends the range of the family back into upper Pennsylvanian times. Use of the taxonomic category "family" may be questioned with justification even though it is a rather remarkable series of fossils, and a few

[1]Issued September 20, 1948.

comments on the inter-relationships of the various genera will be offered following the description of the specimen.

Protoösmundites Wilsonii gen. et sp. nov.

The single specimen consists of a well-preserved siphonostele and a portion of what apparently was the inner parenchymatous cortex, including numerous leaf traces.

The wood is cylindrical, 2 mm. in diameter, there being no evidence of cambial activity (fig. 1). Within this is a well-preserved core of parenchymatous pith. As may be noted in the transverse and longitudinal sections (figs. 1, 2, 6), the pith cells are essentially isodiametric and uniformly thin-walled, no evidence of tracheidal pitting being apparent. Since the preservation is good there seems to be no doubt that we are dealing with a clearly defined siphonostele and a purely parenchymatous pith. This has an important bearing on the position that the fossil occupies in the Osmundaceae, a point that will be considered later.

The xylem is very slightly crushed but was apparently perfectly cylindrical in life, and approximately .5 mm. in radial thickness. It is composed entirely of scalariform tracheids[1], there being no admixture of parenchyma cells. The protoxylem elements appear as numerous, slightly extruding groups around the outer periphery. The first-formed cells are very nearly exarch, but their exact position is obscured by the imperfect preservation in this region and by the abundance of leaf traces. However, the latter appear uniformly centrarch immediately after their departure (fig. 5), and since they depart in such rapid succession it is not possible to distinguish protoxylems of the stele from those of the traces.

The protoxylem cells are markedly smaller than those lying immediately within and could not have been more than 2 or 3 cells of being exarch in position. The xylem cells range from 12 μ in diameter for the protoxylem elements to more than ten times as large for the largest (innermost) metaxylem cells. Two of the latter (fig. 1) measured 180 x 120 μ and 220 x 100 μ.

The secondary thickening of the tracheidal walls (fig. 4) is uniformly scalariform with the exception of the small outermost cells, which may best be termed annular. The latter differ from the metaxylem cells in that the secondary thickenings consist of finer rings and apparently lack any border.

[1]In Part III of their series on the Osmundaceae, Kidston and Gwynne-Vaughan state that the xylary elements in both recent and fossil species of the group are actually vessels since perforations exist between pits of adjoining cells, and Gwynne-Vaughan considered this problem more generally in another paper (1908). We are inclined to doubt that the perfection of preservation in all fossils assigned to the family allows positive determination on this point. Even though the central membrane did disintegrate with maturation of the cells, to apply the term vessel would be misleading since in other respects these cells are more closely comparable with normal scalariform tracheids of other vascular cryptogams and gymnosperms than with the vessels of the angiosperms.

The leaf traces departed slowly, forming a very acute angle with the stele, as is clearly shown in radial longitudinal sections (fig. 6). This is also indicated in transverse sections, where, at any one point, a large number of traces may be noted (fig. 1). It is unavoidable that most of the traces are cut more or less obliquely, yet where nearly perfect transverse sections are available it is clear that the protoxylem occupies a central position (fig. 5). The secondary thickening of the leaf trace elements is the same as that of the outer stelar cells, consisting of very fine annular bands (fig. 3).

Aside from the leaf traces, the only extra-stelar tissue that is preserved is a portion of the inner parenchymatous cortex, the cells of which are uniformly thin-walled and of essentially the same shape as those of the pith although considerably smaller (figs. 1, 6). The decayed area between this tissue and the xylem was probably occupied by phloem, pericycle, and the innermost border of the cortical tissue.

Diagnosis of Protoösmundites: Stem with a small siphonostele of nearly exarch protoxylem tracheids, large scalariform metaxylem tracheids, and a parenchymatous pith; no secondary wood and the primary wood composed of tracheids only; leaf traces small and numerous as in *Osmunda* with a central protoxylem, the cylindrical form of the trace being retained for some distance through the cortex.

Locality: Coal mine of the What Cheer Clay Products Co., one-half mile west of What Cheer, Iowa.

Horizon: Des Moines Series, Pennsylvanian.

Discussion:

The affinities of this fossil appear to lie with the early representatives of the Osmundaceae. In order to clarify our views concerning this probable position it seems desirable to review very briefly certain of the fossils described by Kidston and Gwynne-Vaughan in their monograph on the Osmundaceae.

Six species of *Osmundites* are described from widely separated localities extending from the Jurassic into early Tertiary horizons. In the lower Pliocene (or upper Miocene) *Osmundites Schemnitzensis* from Hungary, and O. *Dowkeri* from the lower Eocene of Herne Bay, Isle of Wight, the xylem cylinder consists of separate strands and surrounds a parenchymatous pith. These relatively recent species are strikingly similar to the modern members of the Osmundaceae. In the upper Jurassic O. *Kolbei* from Cape Colony a comparable xylary structure is present but of special note is the presence of irregularly shaped tracheids in the central tissue, the latter being, in fact, a mixed pith. In the Jurassic O. *Dunlapi* from New Zealand the stele differs from all of the more recent species in having a continuous xylary ring. However, as the central tissue was not present, it is not known whether it was strictly parenchymatous or mixed.

Still earlier genera which are assigned to the family, *Zalesskya* and *Thamno-*

pteris, from the upper Permian of Russia, possessed a stele that was differentiated into two xylary zones. In *Zalesskya gracilis* it consists of an outer ring of elongate tracheids and an inner zone of shorter, nearly square-ended, pitted elements. *Z. diploxylon* is similar, although the contrast between the two xylary zones is more marked, the elements of the central xylem being of relatively greater diameter, shorter, and with transverse walls. In *Thamnopteris Schlechtendalii* the central xylem consists of reticulately pitted cells in contrast to the more regular porose cells of *Zalesskya gracilis*. It should be noted that in all three of these species the centermost portion of the stele had been lost through decay. However, Kidston and Gwynne-Vaughan note that: "As regards *Zalesskya diploxylon*, at any rate, we feel convinced that the central xylem occupied the whole of the center of the stele in the living plant. Further, we accept the deduction suggested by this conclusion, *that the vascular anatomy of the Osmundaceae must be derived from a protostele with a solid central homogeneous xylem mass*." (II, p. 229).

This group of fossils, similar in the organization of their petiole structure, seems to present, through the evolution of a protostele to a specialized siphonostele, a clear-cut line of Osmundaceous ancestors going back to the upper Permian. Although *Protoösmundites Wilsonii* appears to lie closer to this alliance than any other series of ferns it is apparent that it does not fit perfectly into the sequence. If *Zalesskya* and *Thamnopteris* are typical of the family for the period one would expect, in this upper Pennsylvanian species, a somewhat less advanced parenchymatization of the pith. Furthermore, *Protoösmundites* differs from the previously described genera in that the scalariform thickenings of the xylary elements extend across the lateral wall rather than being separated into two or more series. It is not surprising, however, that in this earliest representative a somewhat simpler organization should prevail in this respect.

With regard to the leaf traces, it seems especially significant to note that *Osmundites skidegatensis* (Lower Cretaceous of British Columbia), considered to be the most advanced species, living or fossil, presents a leaf trace "very large, and it is already strongly curved, even while still in the parenchymatous inner cortex of the stem." (Kidston and Gwynne-Vaughan, 1907, p. 772). This is quite in contrast to the upper Permian genera *Zalesskya* and *Thamnopteris*, where the traces remain oval-shaped with a deeply immersed protoxylem for some distance through the inner cortex. Judging from a comparison of our specimen with Kidston and Gwynne-Vaughan's figures of these Permian genera the retention of the centrarch form of the trace is even more pronounced in the Iowa fossil. While further comments can be little more than speculative it appears that the petiole structure in *Protoösmundites* is distinctly primitive, pointing to a frond that was correspondingly less specialized in its general morphology. Until further evidence may confirm or refute it we are inclined to look upon this fossil as either an early representative of the Osmundaceae proper or a member of an associated line leading up from the Coenopterid complex.

Acknowledgement:

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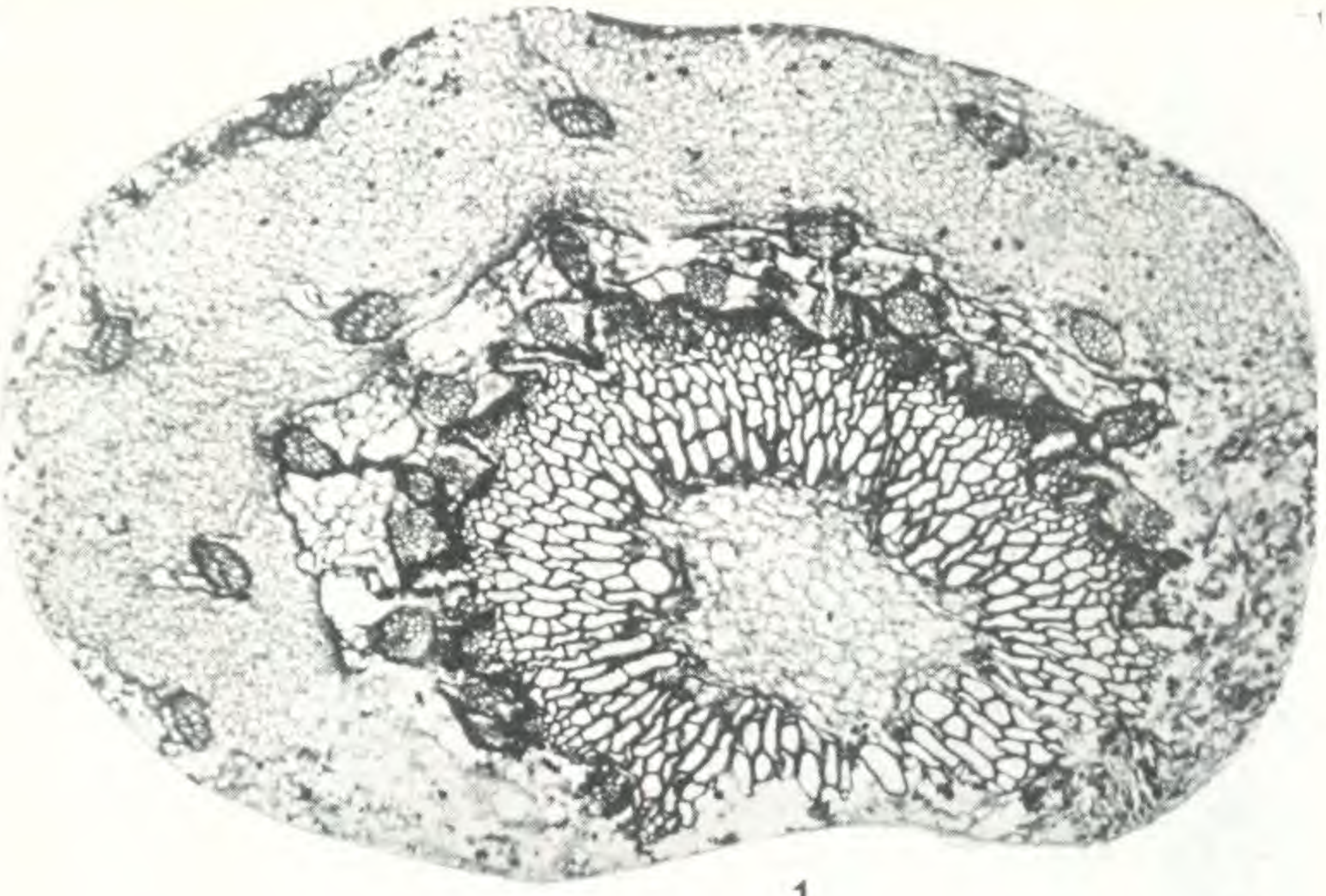
Explanation of Plate

PLATE 9

Protoösmundites Wilsonii

Fig. 1. A transverse section of the specimen showing central pith, wood, leaf traces and parenchymatous cortex. Slide 1521, × 21.

Fig. 2. A radial longitudinal section showing the scalariform nature of the xylem elements: *p*, pith; *m*, metaxylem; *px*, protoxylem. Slide 1518, × 100.



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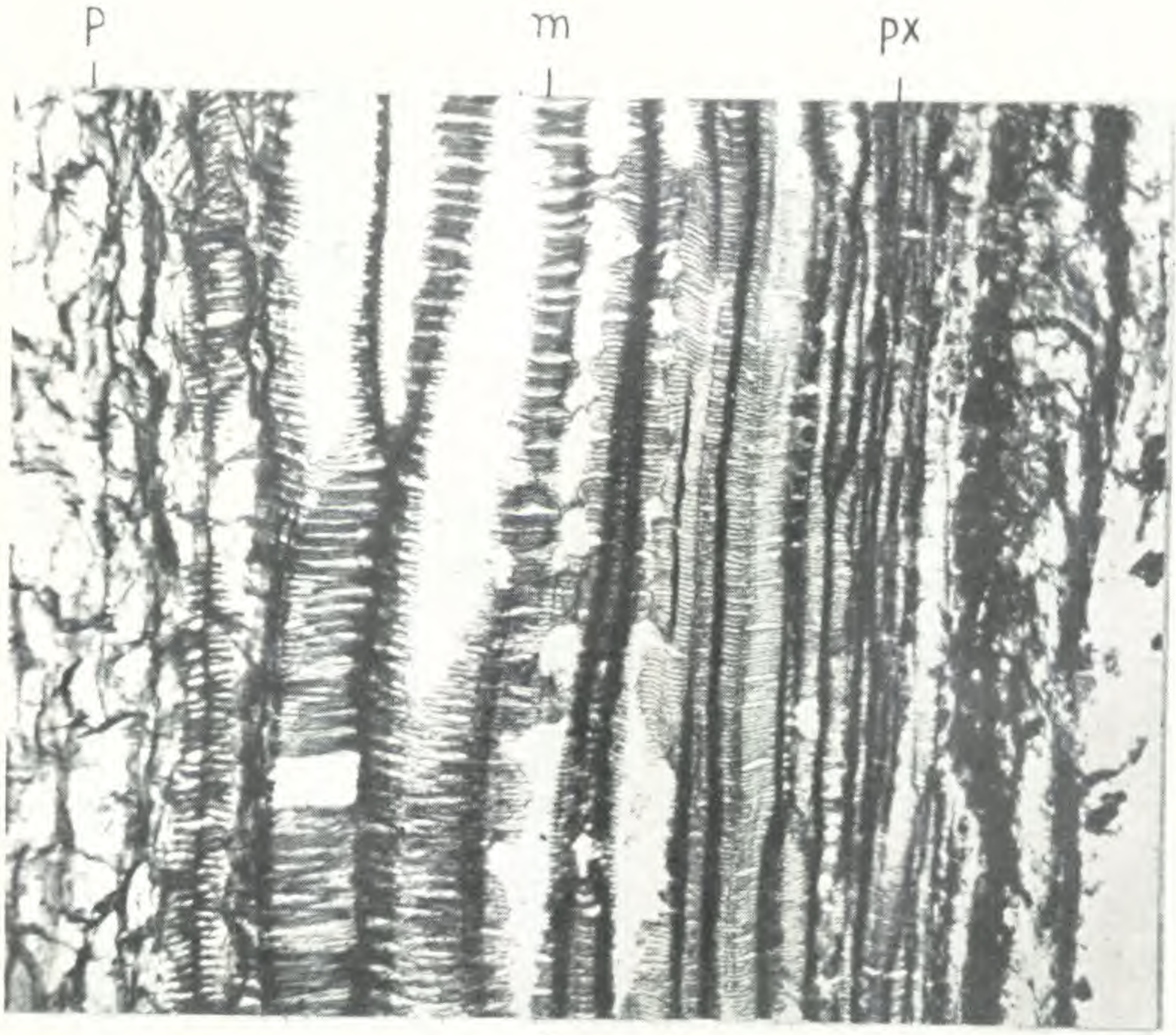
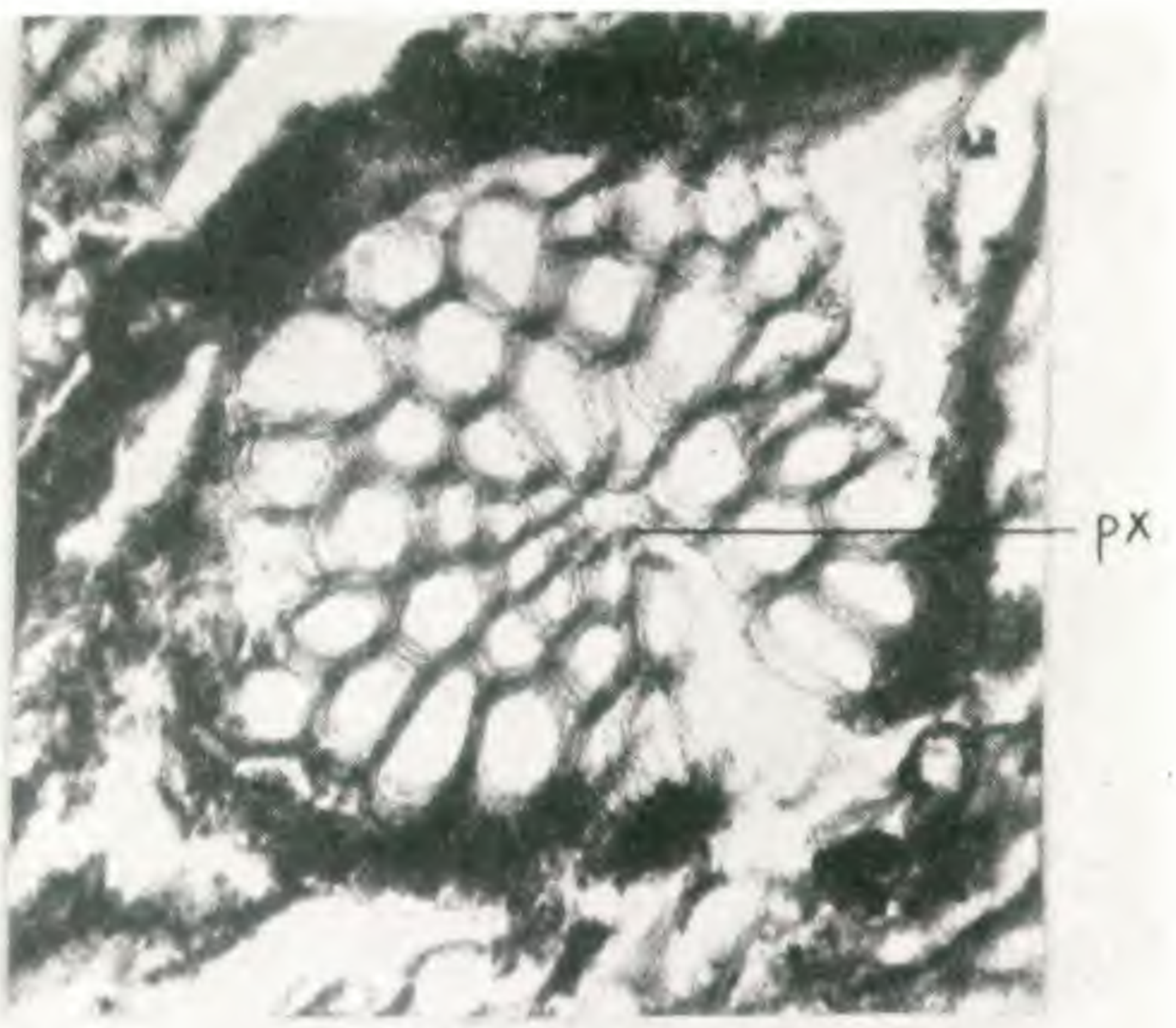


2

ANDREWS & BAXTER—*PROTOOSMUNDITES WILSONII*

3



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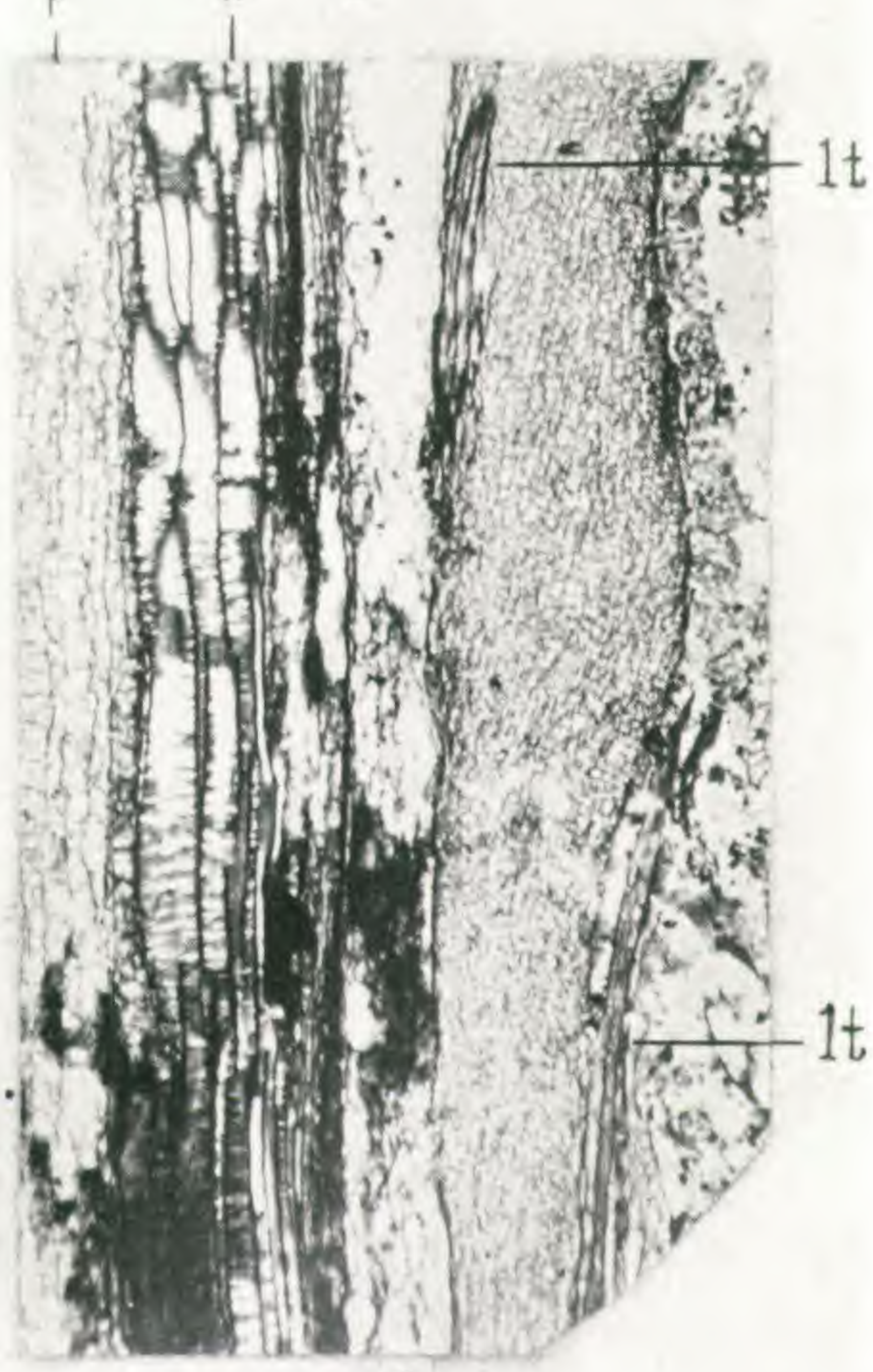

6

ANDREWS & BAXTER—*PROTOOSMUNDITES WILSONII*

Explanation of Plate

PLATE 10

Protoösmundites Wilsonii

Fig. 3. A leaf trace in longitudinal section showing the fine annular thickenings. Slide 1518, × 300.

Fig. 4. Radial view of two metaxylem tracheids. Slide 1515, × 210.

Fig. 5. A leaf trace shortly after its departure from the stele: *px*, protoxylem. Slide 1520, × 230.

Fig. 6. A radial longitudinal section through the stem: *p*, pith; *x*, xylem; *lt*, leaf trace. Slide 1514, × 11.

A CROSSOTHECA FROM NORTHERN ILLINOIS

HENRY N. ANDREWS
AND SERGIUS MAMAY

During a collecting trip to the famous nodule-producing strip mines south of Chicago, in April, 1947, a specimen of *Crossotheca* was obtained which displays both fertile and sterile portions of a frond in organic connection. From a comparison with the American and British fossils assigned to this genus our specimen appears to represent a new species.

A good deal of interest has been shown in *Crossotheca* and supposedly related fossils since it is felt that they are microsporangiate fructifications of certain Pteridosperms. The general problem of the affinities of these fructifications has been considered at length by a number of previous workers and need not be repeated in detail here. About a dozen species of *Crossotheca* have been described, and while certain of these are imperfectly known with reference to the structure of the synangia, the morphology of the sterile foliage, and the general organization of the frond, it is evident that it was a large and varied genus. Judging from the work of Lesquereux, Kidston, Crookall, and others it seems clearly established that in some species the sterile portion of the fronds was of the *Pecopteris* type and in others of the *Sphenopteris* type.

It is not possible to make satisfactory comparisons with all of the previously described species since in some instances spore measurements are not given or the sterile pinnules have not been found attached.

Crossotheca McLuckiei sp. nov.

The single specimen on which this description is based consists of the terminal portion of a fertile penultimate pinna with portions of three sterile pinnae at its base. It is not possible to say what fraction of the entire frond is represented but it is significant that the sterile and fertile portions are in organic connection.

The entire specimen is 6.5 cm. long (fig. 1), including the sterile portion at the base. It is terminated by a fertile pinnule, below which lie five or six lateral single pinnules, and below these are pinnae consisting of from three to five fertile pinnules each. The base of the specimen is terminated by three sterile ultimate pinnae, two of which are shown in fig. 2.

The fertile pinnules are about 3 mm. long and 1 mm. wide and apparently consist of a much-reduced "lamina" bearing up to 20 sporangia in the usual marginal fashion for *Crossotheca.* The sporangia are not well preserved, but when shown in side view appear to have not exceeded 1.5 mm. in length. The spores are mostly uniform in size, being spherical, 70 μ in diameter, with a distinct trilete commissure and a very faintly warted exine (fig. 5). A few spores have been observed that are appreciably smaller (fig. 6) than the others, these measuring 45μ.

[1] Issued September 20, 1948.

Origin: Collected from an old "spoil" near the entrance of the miner's Recreation Area, north of Coal City; base of the Carbondale formation, middle Pennsylvanian.

Type specimen: No. 5005, preserved in the paleobotanical collections of the Henry Shaw School of Botany.

Discussion:

In 1902 Sellards described two species of *Crossotheca* from Mazon Creek, *C. trisecta* and *C. sagittata* (*Staphylopteris sagittatus* Lesquereux). The fertile pinnules, as a whole, as well as the sporangia, of *C. sagittata* are much larger than those of *C. McLuckiei,* and the fertile foliage appears to be more distinctly pecopterid in form. *C. trisecta* differs in that its spores are almost exactly half the size of those from our specimen, and the sterile foliage, according to Sellards, is similar to that of *C. sagittata.* There seems to be no question that the specimen described here is distinct from these two.

Of the Crossothecas considered by Kidston in his monographic review of the genus (1923) *C. communis* (Lesquereux) Kidston seems to be the most closely comparable to our specimen. According to Kidston this species is rare in Britain and was originally based on sterile *Sphenopteris* foliage from American material. The sterile pinnae of *C. communis* (see Kidston, pl. 89, fig. 9b) resemble our specimen but unfortunately measurements of the sporangia and spores are not given for *C. communis.*

Whether all of the fertile specimens that have been described as *Crossotheca* are naturally referable to a single genus may be questioned. Being compression species there are certain structural details about which we would like further knowledge. However, it seems likely that all are closely comparable in the general organization of the fertile pinnule. Although there is appreciable size difference in the spores, their spherical shape and the "minute warty thickenings" that characterize the wall are remarkably uniform in most species. On the other hand, the range in form of the sterile pinnules is equally striking. In *C. Schartzlarensis* the pinnules are very finely divided similar to those of *Rhodea;* in *C. communis, C. McLuckiei,* and *C. Hoeninghausi* they are of the *Sphenopteris* type; in *C. pinnatifida* they are closer to *Neuropteris;* and in *C. Boulayi* closer to *Pecopteris.*

The specimen is named for Mr. John L. McLuckie in recognition of his continued interest in the fossils of the Mazon Creek region and for his generous services as guide on numerous collecting trips.

Literature cited:

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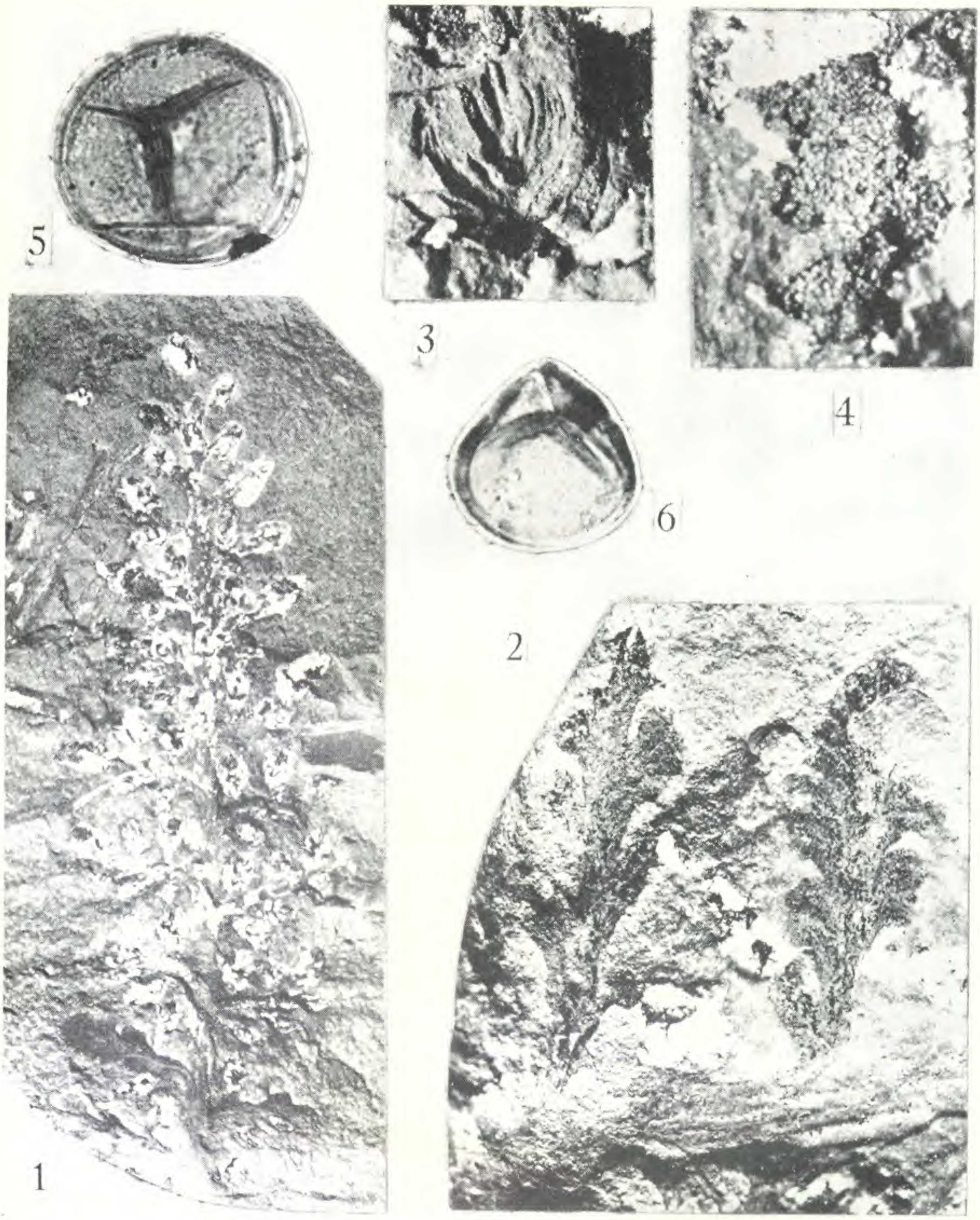

Explanation of Plate 11

Crossotheca McLuckiei

Fig. 1. The entire specimen enlarged × 1.5.
Fig. 2. Two sterile ultimate pinnae shown at the lower left of fig. 1, × 4.5.
Fig. 3. A fertile pinnule from which most of the spores have been shed.
Fig. 4. Portion of a fertile pinnule showing crushed sporangia in side view.
Fig. 5. A representative spore, × 400.
Fig. 6. A smaller spore (see text), × 400.

A NOTE ON *FOMES IDAHOENSIS* BROWN

HENRY N. ANDREWS

About a year ago two specimens of the late Tertiary polypore, *Fomes idahoensis* Brown, were described (Andrews and Lenz, 1947) which had been collected the previous summer south of Bruneau, Idaho. In the summer of 1947 the same locality was re-visited by Mr. S. H. Osgood, of Rupert, Idaho. He obtained a number of additional specimens all of which are referable to the same species, although they represent much larger sporophores than have been reported formerly and indicate quite clearly that they were perennial plants.

Of these newly acquired specimens, one (No. 5002) is a fragment of a sporophore in the first or possibly second year of growth, the maximum length of the pores being about 28 mm. long. This specimen measures approximately 14 by 6.5 cm., being somewhat larger than previously described ones although it is not a complete bracket.

Of particular interest are specimens No. 5003 and No. 5004, which are pore fragments only. While these retain none of the context and offer no clues as to the size of the bracket as a whole the pores in both attain a length of 70 mm. Judging from the pore size these specimens, fragmentary though they are, compare closely with the previously described specimens (Andrews and Lenz, 1947), as well as the type material (Brown, 1940), from the same locality. They seem to offer conclusive proof that the original designation of these fossil polypores to the genus *Fomes* (Brown, 1940) was correct. There is a suggestion of "rings" in the pores (No. 5003), indicating four or five years of growth, although these cannot be clearly distinguished.

The author gratefully acknowledges Mr. Osgood's generosity in donating these interesting and rather rare fossil fungi to the collections of the Henry Shaw School of Botany.

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A STUDY OF THE VEGETATIVE ANATOMY OF THE GENUS SPHENOPHYLLUM FROM AMERICAN COAL BALLS

ROBERT W. BAXTER

Introduction

Although the genus *Sphenophyllum* has been described in some of the earliest paleobotanical works and Seward (1898) lists it as one of the best-known fossil plants, the rich source of petrified specimens in the American coal balls has been very largely ignored. The works of Renault and Williamson (1878) did much to make known the inner structure of the stems, roots and leaves of the English and European forms, although gaps were left concerning our knowledge of branching, the attachment of roots, and other anatomical points. It was with the hope, therefore, of contributing to our knowledge of the internal structure of the plants, as well as the desire to make better known the American fossils and to correlate them in so far as possible with the English and French species, that this study was undertaken.

The material on which this study was based was obtained from two sources as follows: The Pyramid mine, two miles south of Pinckneyville, Perry County, Illinois, this horizon being at the base of the McLeansboro series (coal No. 6) and of upper-middle Pennsylvanian age; and The What Cheer Clay Products Co. coal mine, one-half mile west of What Cheer, Iowa. This horizon lies in the Des Moines series of the Pennsylvanian.

Review of Literature

Sphenophyllum, in the form of compressions, has been noted and described by some of the earliest investigators. Solms-Laubach (1891) states, "The genus, owing to its striking appearance, has been repeatedly figured by the old authors." In Scheuchzer's *Herbarium Diluvianum* (1723) there are drawings of stem fragments bearing whorls of small wedge-shaped leaves which were undoubtedly made from specimens of *Sphenophyllum*.

Renault (1878) was the first to link together definitely the petrifactions showing internal anatomy with the well-known leaf and stem compressions. He described three species from petrified material, only one of which, S. *quadrifidum*, has been retained by recent authors. It is supposedly characterized by double groups of protoxylem at each angle of the primary triangle, giving a hexarch structure. However, in examining Renault's original plates and descriptions we have found little evidence of clearly defined hexarch anatomy. His other two species based on petrifactions were S. *stephenense*, which is figured as having two forked and two single leaf traces from each protoxylem angle, and S. *erosum*, which his drawing purports to show with 18 leaf traces radiating out from the stele in all directions. Whatever the 18 "rays" were in the later drawing, we feel certain

that they were not leaf traces though it is possible that they could have been vascular strands to adventitious roots.

Williamson (1874) described two petrified stems with triarch protosteles as species of *Asterophyllites*. In 1895, recognizing their true nature, he redescribed them in detail and with many excellent illustrations, as *Sphenophyllum plurifoliatum* and *Sphenophyllum insigne*. *S. plurifoliatum* did not differ in any important anatomical features from the specimens previously figured by Renault, but Williamson's detailed descriptions clarified the characteristic structure of the genus. *S. insigne* differed in coming from a much lower horizon in the Lowest Carboniferous, supposedly in having fairly consistent continuous parenchyma rays in the interfascicular[1] wood, and in the presence of protoxylem lacunae.

Koopmans (1928) has described two new species, *S. minus* and *S. perforatum*, from the Finefrau horizon of the Netherlands. The former differs from *S. plurifoliatum* in having a smaller protoxylem strand (0.4 mm.), a less concave metaxylem, a narrower fan of fascicular xylem, and smaller interfascicular xylem cells adjoining the metaxylem. *S. perforatum* differs in possessing protoxylem lacunae, smaller metaxylem cells, and more prominent arms to the primary wood triangle. We shall have more to say concerning these species later.

Leclercq (1925) has described *S. Gilkineti* from the upper Carboniferous of Belgium on the basis of two different zones of secondary wood. This species will be treated more fully below when variations of the *Sphenophyllum* stem are described.

With the exception of the six species just mentioned, all of the other *Sphenophyllum* species have been described on the basis of leaf differences observable in compressions. Potonié (1910) lists eight species, while Lesquereux (1880), in his work on the coal flora of Pennsylvania, describes nine variations in leaf form. Five of these he assigns to European species, intimating a close relationship for the plant in the two geographical areas, a fact which finds support in petrified material. Indeed Walton (1940) illustrates (his figure 42) a *S. plurifoliatum* stem type from England which is so similar to the Illinois material that it could have been made from one of our own peels.

Prior to this study there has been almost no attention paid to petrifactions of *Sphenophyllum* in this country. A few investigators have mentioned finding stems of the *S. plurifoliatum* type in American coal balls but no descriptions have been given. Darrah (1939), in dealing with the flora of Iowa coal balls, listed *Sphenophyllum* stems and strobili (of the *S. Dawsoni* type) but did not include any illustrations or descriptions. This neglect is the more surprising since the Iowa and Illinois coal balls contain abundant and excellent specimens. It is a rare coal ball that does not produce at least one or two stems, while some are found with as

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[1]The terms fascicular and interfascicular are used here and throughout the text in the sense originated by Williamson and Scott (1895): fascicular, in all cases, referring to that secondary wood formed opposite the protoxylem groups; and interfascicular indicating the secondary tissue formed opposite the sides of the triangular protostele and between the protoxylem groups.

many as nine or ten stems in an area 3–4 inches in diameter. Consequently we have had the advantage of being able to observe hundreds of specimens in varying stages of growth.

General Description

The external appearance, as evidenced in compressions, is that of a slender stem 1 cm. or less in diameter, with cortical furrows and whorls of leaves which do not alternate from node to node as in *Calamites.* (The most ancient of the *Calamites, Archaeocalamites,* from the Lower Carboniferous did, however, have the same superimposed structures.) The nodes themselves are commonly somewhat swollen while the leaves vary considerably in size and form, a large number of species having been described on the basis of foliar differences. The type on which the genus was founded has wedge-shaped leaves with an entire or very slightly toothed margin. In some species the foliage is deeply dissected, while in others the plants are heterophyllous, bearing both entire and deeply lobed leaves on the same stem. The anatomy of the stem has constituted one of the primary reasons for the isolation of the genus.

Primary Tissues

Transverse sections of the stems show the primary wood to be a solid mass of tracheids, triangular in outline and with the protoxylem occupying the apices of the triangle. The protoxylem tracheids are small (20 μ in diameter), with ring or spiral thickening. The transition to metaxylem is quite abrupt, with a distinct increase in cell size and a characteristic reticulate bordered pitting on both the radial and tangential walls.

Generally most of the plants observed appear to comply with the descriptions of *Sphenophyllum plurifoliatum* Williamson. However, we shall point out several variations from the basic *plurifoliatum* type which seem to indicate that stem anatomy, at least in the internodal region, may constitute a doubtful basis for specific differences.

On the whole, our Illinois specimens are smaller than those described from England and Europe. The largest stem observed was not over 4 mm. in diameter, while Williamson (1895) has indicated that many of the English specimens reached 1 cm. It is of some interest also to note that while Bower (1930) observed primary wood averaging 1 mm. in width (measured from a protoxylem angle across to the opposite fascicular wood) the largest we have been able to secure measures .5 mm., the average size being .4 mm. The Iowa stems (figs, 3, 7, 8, 10 and 11) show the same small primary wood, though some of them (figs. 7, 11) exhibit considerably more secondary wood with larger total diameter than was found in the Illinois specimens.

Immediately adjoining the primary wood there is often a layer, usually one cell thick but sometimes two, of xylem parenchyma which surrounds the entire triangle with the exception of the protoxylem angles (fig. 17).

Figure 1 illustrates a stem which presents the features of S. *plurifoliatum* although showing clearly defined protoxylary canals which hitherto have been observed only in the more ancient S. *insigne*.

The lacunae appear to be the result of a disintegration of the protoxylem tissues, as very often an accompanying disruption is to be noted in the adjoining fascicular wood. From the constancy of their occurrence there is little doubt but that they represented a character of the living plant. Figure 1, showing one of the few stems of this type retaining its epidermis (most of the specimens having only a thick periderm), exhibits deeper and more numerous furrows (in this case eight) than are usual in S. *plurifoliatum*, which commonly has just three deep grooves opposite the sides of the primary triangle. However, none of these specimens just described was found with leaves or branches, and because our studies on the external form of the stem at the node and internode in a definite S. *plurifoliatum* stem showed that there could be very wide differences in size and form it seems wiser, at least for the present, to list this group as one of the variations of the basic *plurifoliatum* type than to attempt to assign it specific value.

Secondary Tissues

The secondary wood is radially arranged around the triangular primary tissues in a geometrical pattern that results in the rows of cells opposite the protoxylems being much smaller than those opposite the metaxylem. Consequently the fascicular wood forms a radiating fan of narrow rows of small cells which gradually increase as their angle of divergence increases until in the outer margin of large stems the two zones are almost identical (fig. 11). According to Williamson (1895) and Scott (1920), this fascicular region has continuous parenchyma rays of a different type from those of the interfascicular wood. However, we have been unable to observe any evidence of this in our material, while indeed some stems (fig. 11) very obviously show identical ray structure to the interfascicular zone.

The tracheids of the interfascicular xylem are in transverse section normally large, rectangular, and with truncated angles, the spaces between them being occupied by groups of small, vertically aligned parenchymatous cells. In radial section these vertical parenchyma cells are connected by many small horizontal ones extending across individual tracheids, forming an effective ray system (fig. 8).

Figures 5 and 6 show an interesting stem in which an injury evidently caused the growth of "fascicular type" wood for over two-thirds of the circumference. The injury appears to have occurred when two rows of secondary wood had been formed and to have caused the cambium to start producing a series of smaller cells. On the side of the stem farthest from the wounding the secondary wood was unaffected. The abnormality is evidently quite similar to *Sphenophyllum Gilkineti* Leclercq, concerning which we shall say more later.

Another secondary wood variant is illustrated in fig. 2. Here an apparent sclerotic growth is seen replacing the usual corner groups of parenchyma. The

Sphenophyllum nature, however, is still obvious in the triarch structure of the primary wood, the deep-seated periderm, and the sclerotic furrowed outer cortex.

The pitting of the secondary wood is similar to that described for the metaxylem except that there are fewer pits in the tangential walls. The pitting presents a good character for recognizing the genus in longitudinal sections, the pits being ovoid to circular and arranged so thickly on the radial walls that they form a reticulate pattern. All previous investigators have described these pits as bordered, but it seems likely that the border must have been quite fragile, since the pits normally appear simply as perforations in the cell wall (fig. 8). Next to the pitting the most distinctive character of the wood is the length of the xylem cells. Although longitudinal sections over 1 cm. long were obtained, it was still impossible to find any trace of end walls, so the question of the true nature of these cells (tracheids or vessels) must remain an open one.

The parenchyma tissues outside the wood are seldom well preserved, being replaced at an early stage by a deep-seated periderm which appears to have arisen first in the pericycle or endodermis and then in successively deeper series within the phloem. Figure 12 illustrates a cross-section showing two layers of periderm, the inner abutting almost directly on the secondary wood so that only a few fragments of phloem and cambium remain. In longitudinal view the periderm can be seen to consist of regular rows of short parenchymatous cells, darker in color than the other stem tissues and appearing to retain considerable cell contents.

The outer cortex in mature stems is often replaced by the thick periderm growths just described. When present it offers a distinctive character in its strongly sclerotic appearance and furrowed outline.

Branching

To our knowledge, branching in the petrified material of *Sphenophyllum* has not been reported up to this time. Williamson (1874) illustrated a specimen showing the base of a lateral appendage, although it seems most likely that it represented a root departure. The vascular tissue followed a horizontal course outward from the stele which, as will be pointed out, appears to be characteristic of the leaves and roots but not of true branches. It was with particular interest, therefore, that we found in the specimens represented in the Illinois and Iowa coal balls three stems exhibiting clearly defined branching, each quite different and distinct.

The first stem to be described is characterized in the internode by the roughly hexagonal shape of the outer cortex and an oval periderm surrounding the triangular woody tissue (fig. 15). As the node is approached both the outer cortex and the inner parenchyma layers immediately surrounding the xylem become almost spherical (fig. 16). A short distance above this the general form molds itself to that of the woody cylinder and becomes triangular throughout (fig. 18). At this stage the first evidence of branching is seen in the out-thrusting of segments of pericycle and phloem tissue through the surrounding periderm and cortex

at points opposite the protoxylem angles. There also appear at this time swellings in the periderm, approximately along side of each of the three protoxylem groups, two of them on each side of the triangle. Next, the over-all shape of the stem becomes more definitely triangular and horizontal vascular strands appear extending out from the protoxylem into the three corners and also into the six swellings on the sides (fig. 19). In the next peel (fig. 20) we see that the six side vascular strands lead into the bases of leaves while the fascicular tissues at the corners have extended through the outer cortex at a sufficient angle from the horizontal to exhibit most of their area in transverse view. These large corner vascular bundles, surrounded by a thin layer of phloem and pericycle and what appears to be tissue from the periderm, are soon pushed out beyond the outer cortex of the main stem. At this stage adventitious roots are produced abundantly and appear passing out through the cortex of these vascular bundles in all directions (figs. 20 and 22). The following stage finds the three branches separated from the main stem by their own sclerotic outer cortex. The numerous adventitious roots are still evident while the stem is observed to have regained its original hexagonal form (fig. 21). Our last illustration of this series shows the central portion of one of the branches, some distance from the main stem, in which the characteristic triarch stele structure is beginning to appear (fig. 23).

In the second specimen the stem produced just one branch instead of three, and there is no evidence of a node or leaves in the vicinity of the branching. The offshoot is first observed as a large mass of fascicular wood coming off from a protoxylem corner of the primary triangle. Its angle of departure from the stem is quite acute so that it maintains an approximate vertical position throughout its passage. The main stem, instead of the triangular shape characteristic of our other specimen, is a flattened oval with the elongation in the direction of the branching (fig. 26). The preservation of the branch was so very poor shortly after it became independent that it was not possible to follow it for a sufficient distance to show a node; however, fig. 27 illustrates its appearance at the point of separation from the stem. The typical sclerotic furrowed outer cortex is evident, and while the primary wood does not as yet exhibit the usual triangular form of our previous specimen (in which the preservation was considerably better) this character did not develop until some distance from the main stem. Probably the most curious feature of this specimen is the production of two curved appendages from the other two corners of the primary triangle at the same vertical position as the start of the branch trace (fig. 25). The vascular tissue in these appendages is horizontal (90° angle to the main stem) and the structures themselves are apparent for some distance in a horizontal position. They are quite small and with a thick cortex, at least at the base where they depart from the stem, so they obviously could not be leaves. We are, therefore, inclined to regard them as modified roots which functioned as specialized appendages enabling the vine-like *Sphenophyllum* to cling or prop itself upon supporting surfaces.

The third form of branching observed is illustrated in figs. 7 and 10 and appears to have consisted of an unequal dichotomy with the branch being considerably larger than the main axis. That the larger structure constituted the branch was proved by longitudinal sections showing the angle of departure. This feature would seem to offer additional evidence of the vine-like nature of *Sphenophyllum*.

Leaves

The leaves were borne in whorls at the nodes and were fused for a short distance from the base (fig. 29). They were in multiples of three, and six appears to be the average number of the Illinois and Iowa specimens. In the six-leaved specimens vascular tissue was supplied by means of V-shaped traces given off from each angle of the primary triangle, one trace going into each leaf and dividing dichotomously in the outer cortex or the leaf base. Figure 3 shows an unusually perfect nodal section with all six leaf traces traversing the cortex into the leaf bases. In the destruction of the inner tissues the connection of the traces to the protoxylem angles has been lost; however, fig. 32, a nodal section of a smaller stem, comes fairly close to showing the attachment.

The internal anatomy of the leaf appears to have been relatively simple. The outstanding feature in the petrified material is the conspicuous ring of fiber strands enclosing the 7–8 tracheids which form the vein (fig. 24). The mesophyll seems to have been undifferentiated and seldom of more than one or two cells in thickness. The lower and upper epidermal layers were one cell thick and with no apparent cuticle. No stomata were observed though they have been reported by Renault (1878).

Roots

The roots were first identified and investigated by Renault (1878). The identification was made on the basis of relatively large roots which possessed the same distinctive secondary wood as the stems. Since then they have been noted and figured by various investigators but never organically connected with the stems.

Early in the present work it was noticed that surrounding many of the *Sphenophyllum* stems were small roots averaging .3 mm. to .4 mm. in diameter. These consisted of 2–7 small tracheids, a well-defined endodermis, 2–3 layers of large parenchymatous cortex cells (average diameter 50 μ), surrounded by a single-layered epidermis of conspicuously large cells (diameter 40 μ), with abundant root hairs (figs. 9 and 30). From two coal balls we were able to secure peels which contained, along with the *Sphenophyllum* stems, almost homogenous masses of these roots in which all sizes were represented from the smallest, described above, to mature roots such as illustrated in fig. 28. These showed a nearly continuous series of developmental stages, indicating conclusively that these small previously undescribed roots represent the initial stage of the already known mature specimens. Secondary growth appears to have been initiated very early and to have

produced rapidly the characteristic square tracheids with the groups of parenchyma cells at their angles. Since the cambial growth was from a small rounded primary strand the radiating rows of secondary wood are uniform and are not differentiated into fascicular and interfascicular zones as in the stem where the growth was from a triangular base. A phellogen also became active in the endodermis at an early stage and by the time that 4–5 layers of secondary wood had been produced the periderm had usually grown to the degree that the cortex and epidermis were lost. Thus these latter tissues are observable only in the youngest roots (fig. 30).

In none of our specimens do we find much support for the belief that these roots were diarch or even monarch in the strict sense. Figure 30 illustrates a small root in which there are approximately six tracheids composing the primary wood. There is no apparent growth of metaxylem, while there does seem to be, even at this early stage, the initiation of secondary growth as evidenced by the large tracheids to be seen on both sides of the primary tissue.

In order to establish beyond any doubt the *Sphenophyllum* origin of these roots particular attention was paid to finding some in actual connection with the stems. In making a longitudinal series of peels through a well-preserved specimen, the structure illustrated in fig. 35 was discovered. Here we have a root identical to the small ones described above, within the middle cortex of a *Sphenophyllum* stem. The conspicuous epidermis, large cortical cells, and dark endodermis are clearly recognizable. The evidence seems to be quite definite that the adventitious growth of these roots could and did occur on any part of the stem but that it was ordinarily most abundant in the vicinity of the nodes. As previously mentioned in the description of branching, many of these small roots were observed being given off at the base of the newly formed branches (figs. 21 and 22).

In addition to the above instances, figs. 31 and 33 show a longitudinal section of a *Sphenophyllum* stem with what we believe to be extremely large roots being given off opposite each other and immediately dividing into groups of small roots. Figure 31 shows the vascular strand passing horizontally from the stem into the appendage. It is felt that this is an important diagnostic character since, as indicated earlier, the vascular bundles passing to the branches always leave the stele at an acute angle. Therefore only the leaves and the roots exhibit this horizontal passage of the vascular tissue, and in this case we are clearly not dealing with a leaf.

The pitting of the tracheids of both small and large roots was observed in longitudinal radial sections. The reticulate bordered pitting, so common on the radial walls of the stems, was clearly evident in both.

Discussion

It is apparent that although *Sphenophyllum* has been described as "one of the best-known fossil plants" (Williamson and Scott, 1895), and has been illustrated by numerous authors since Renault's time, there still remain phases of its general organization that need clarification.

Our three stems, while presenting identical anatomy in the internode region, show quite distinct differences at the point where the branch or branches are given off. In one we have three offshoots at a conspicuous node, while in another just a single branch is produced with root-like appendages springing from the other two protoxylem angles and with no sign whatever of any node or leaves, and in the third there is an unequal dichotomy with the branch being the larger. In all three the branch vascular tissue originates from the main stele at an acute angle instead of a right angle, as is characteristic of the leaves and roots, and the first two specimens described show typical sclerotic cortex; while the specimen in which we were able to follow the branch for some distance presented a clearly outlined triarch protostele. Therefore we have either the anomaly of three distinct branching patterns on one plant or significant taxonomic characters which are not correlated with any other observed differences in stem anatomy.

It would seem that the anatomy of the internode (which makes up 99 per cent of the sections usually obtained) is an unreliable key to specific segregation, in that it fails to emphasize sufficiently such differences as may exist in other parts of the plant, or may, on the other hand, present misleading supposedly specific differences. Examples of this latter point are illustrated in figs. 2 and 5 where the variations are, we feel, due to some local outside influence.

Further difficulty in attempting to define additional species on stem anatomy is well shown in the specimen illustrated in fig. 15. Here the internodal structure is identical in every way to S. *plurifoliatum* but at the node is shown clearly to have only six leaves, while both Scott (1920) and Williamson and Scott (1895) state repeatedly that their specimens had many leaves, probably around 18. Lacking nodal sections they could not make an exact count but evidently they had considerable evidence from leaf parts preserved with the stem. Possibly they were working with a different species than we have illustrated, but one of strikingly similar wood anatomy.

All points considered, it seems more feasible, at least for the present, to allow the species S. *plurifolium* as described by Williamson and Scott to cover nomenclature needs of these Illinois and Iowa petrified stems. We do feel that a short description of the structural variations is worth giving here. Then, if additional research reveals correlating characters in other plant organs they could be given specific importance.

Type 1.—Characterized by constant presence of protoxylem lacunae. Protostele averages .4 mm. from angle to opposite side of triangle. Large metaxylem cells with occasional xylem parenchyma on margin. Outer cortex in internode region more or less circular in outline with 8–10 deep furrows (fig. 1). This type resembles S. *perforatum* and S. *insigne* in its possession of protoxylem lacunae, but in all other respects it is identical to S. *plurifoliatum*. The characters separating the aforesaid species from S. *plurifoliatum* are, in our opinion, doubtful.

In examination of Williamson's figures and of *Sphenophyllum insigne* peels from the Calciferous Sandstone horizon we have been unable to observe the continuous medullary rays in the interfascicular wood. This feature, along with the protoxylem lacunae, supposedly distinguished the species, while the slight differences in size and form of the primary wood listed by Koopmans for S. *perforatum*, in our opinion, are too variable to be reliable.

Type 2.—No protoxylem lacunae. Definite xylem parenchyma between metaxylem and interfascicular wood. Large metaxylem cells, equal in size or larger than secondary wood. Protostele size averages same as above. External form of outer cortex at the internode is hexagonal with a deep furrow opposite each side of triangular protostele. S. *minus* Koopmans would fall in this group. The differences in the concavity of the metaxylem, shape and size of the fascicular and interfascicular wood are not, we feel, constant enough in any of the forms to be reliable characters. The pure size difference of the protoxylem that has been observed in the Netherlands and Illinois and Iowa forms is not in itself sufficient reason for separating them from S. *plurifoliatum*.

Type 3.—Abnormal growths resulting from injury to stem (figs. 5 and 6) and sclerotic growths replacing usual corner parenchyma (fig. 2). Not really types at all but specimens which may show up with some frequency and which should be recognized for what they are. S. *Gilkineti* is, we feel, identical to the type showing abnormal growth resulting from wounding. Miss Leclercq's type specimen, as she stated, also had obviously been injured in growth and while she recognized the possibility of its being an abnormal growth her reasons for assigning specific value were as follows:

> Nous avons longtemps hésité dans l'interprétation des nos échantillons des figures 2 et 3. La présence de deux bois secondaires différents dans la tige complète de la figure 2 pouvait elle s'expliquer uniquement par l'excitation des tissus végétaux due aux buessures, ou représentait-elle la structure normale d'un nouveau type de *Sphenophyllum*? [p. 33].
>
> La découverte, dans le travail de Williamson, d'une coupe transversale très bien conserveé, d'un *Sphenophyllum* identique à celui de notre figure 2, a levé le doute quant à l'interprétation; nous sommes bien en présence d'une espèce nouvelle. Il est en effet invraisemblable de supposer que le *Sphenophyllum* de Williamson ait pu etre blessé lui aussi de telle manière qu'il reproduise une structure identique à celle de notre S. *Gilkineti*. [p. 33].

With our discovery of a stem showing the two zones of secondary wood accompanied by wounding it no longer seems "improbable" to suppose that Williamson's figure was also of an injured stem.

There is still much to be learned from more extensive studies of the petrifactions of *Sphenophyllum*. It is undoubtedly a larger group and more diversified than has been so far suspected. While the anatomy of the internode seems unreliable as a basis for specific distinctions (at least from the present material) the discoveries of additional nodal sections may be expected to show wide variations in leaf and branch form of possible specific value

The most important implications, we believe, to come out of the present study are additional facts for the relationship of *Sphenophyllum* to Equisitales. As Jeffrey (1899) points out "protostely and siphonostely may occur in different

genera of the same family, and even different species of the same genus." So with the observance in *Sphenophyllum* of fairly common protoxylem lacunae and origin of the branches *between* the leaves the only major distinction separating the groups is the peculiar parenchyma ray system of *Sphenophyllum*, and in this we have seen how occasional horizontal conjunction of the radiate parenchyma may produce structures similar to normal rays.

Therefore, on the basis of vegetative anatomy, we are inclined to agree with Jeffrey that there is no valid reason from excluding *Sphenophyllum* from the Equisitales and that it should be regarded as an offshoot from the group ancestor in which the primitive protostele and superimposed internode and leaf whorls have been retained.

Acknowledgment

Thanks are due Dr. Henry N. Andrews for his criticism and advice during the progress of the present work. We are also grateful for the continued goodwill of the Binkley Coal Company and their excellent cooperation in our collecting work.

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Explanation of Plate

PLATE 12

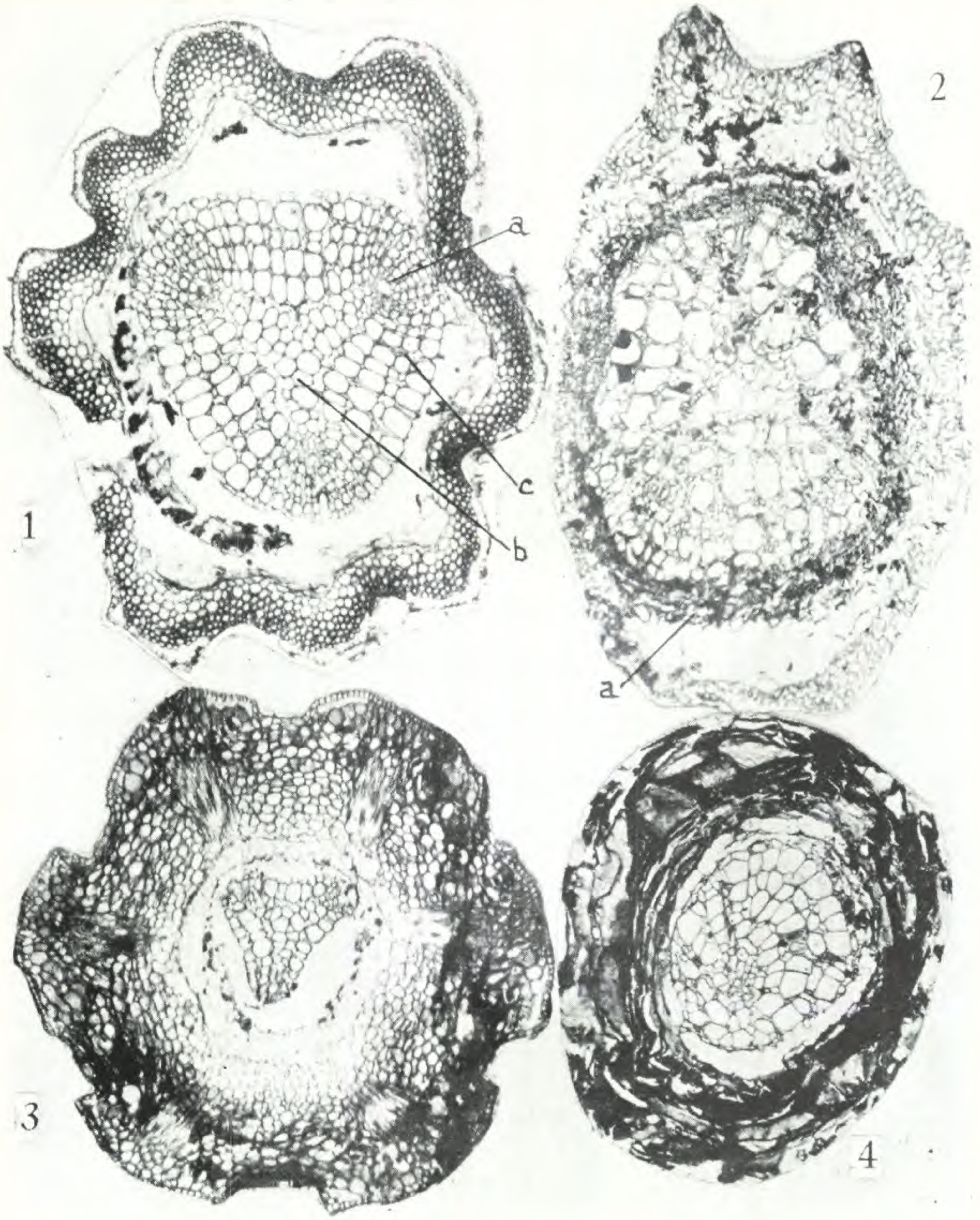
Sphenophyllum plurifoliatum

Fig. 1. Transverse section of stem showing eight cortical furrows: *a*, protoxylem lacuna; *b*, metaxylem; *c*, parenchyma ray extending through three rows of secondary wood. From slide 1523, × 17.

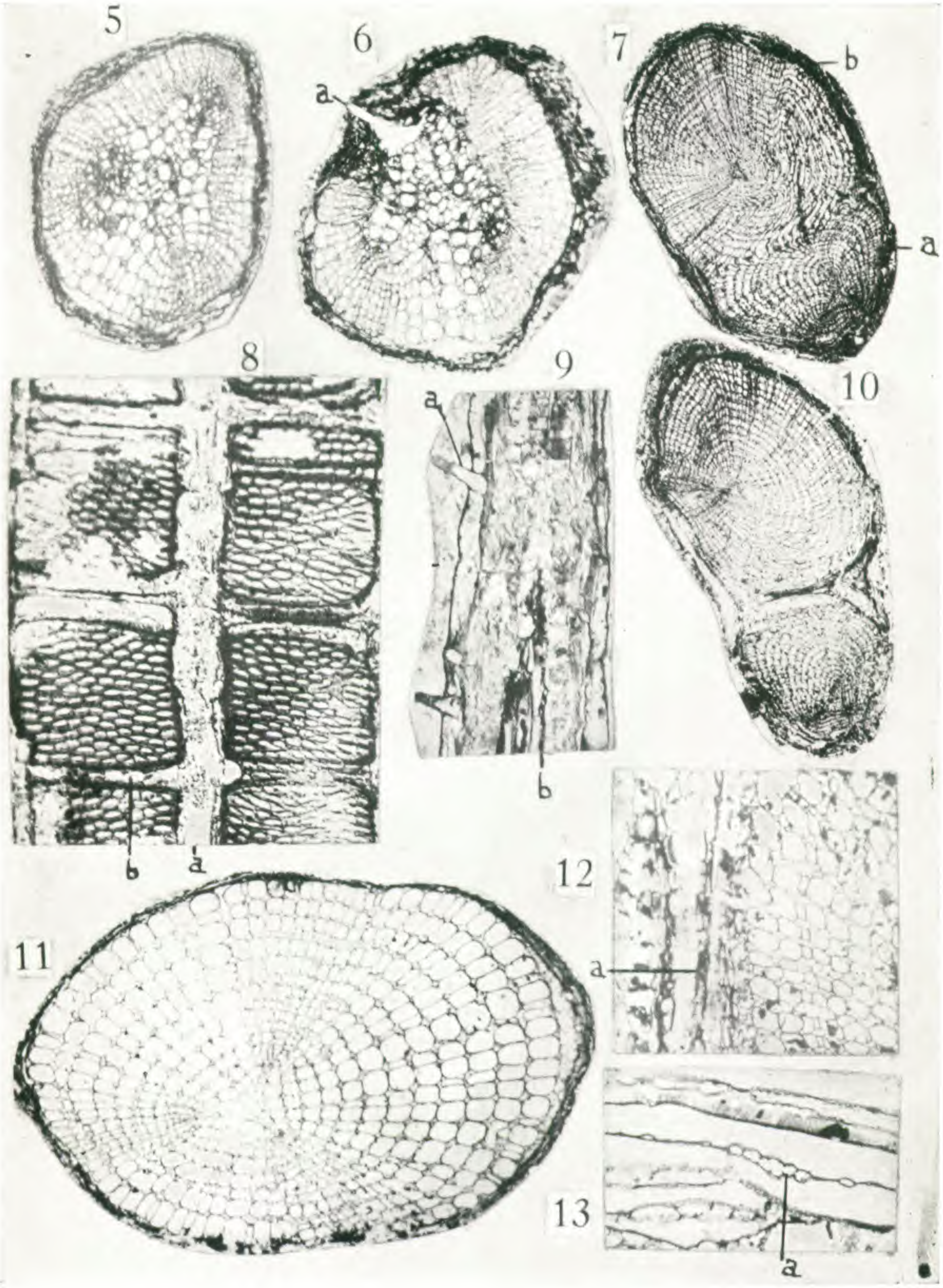
Fig. 2. Transverse section of stem showing sclerotic type of stele: *a*, internal periderm. From slide 1524, × 34.

Fig. 3. Transverse section of a stem at the node showing all six leaf traces passing into the leaf bases. From slide 1525, × 15.

Fig. 4. Transverse section of a medium-sized root showing thick periderm layer. Secondary wood unevenly developed. From slide 1526, × 60.



BAXTER—*SPHENOPHYLLUM PLURIFOLIATUM*



BAXTER—*SPHENOPHYLLUM PLURIFOLIATUM*

Explanation of Plate

PLATE 13

Sphenophyllum plurifoliatum

Fig. 5. Transverse section of stem showing two zones of secondary wood on two sides of the primary wood triangle with normal development on the third side. From slide 1527, × 17.

Fig. 6. Transverse section of same stem as in fig. 5 at a slightly different level showing wounding of the tissues at the point of origin of the second zone of different growth. From slide 1528, × 17.

Fig. 7. Transverse section of a stem showing unequal dichotomy: *a*, main axis; *b*, branch. From slide 1529, × 4.

Fig. 8. Longitudinal-radial section of two rows of inter-fascicular tracheids (vessels?) showing characteristic reticulate pitting: *a*, area occupied by vertical parenchyma cells; *b*, one of horizontal-radiate parenchyma cells. From slide 1530, × 85.

Fig. 9. Longitudinal section of small *Sphenophyllum* root: *a*, root hair; *b*, endodermis. From slide 1526, × 45.

Fig. 10. Same stem as in fig. 7. Forking of stem almost complete; orientation same as above. From slide 1531, × 4.

Fig. 11. Transverse section of a stem with approximately twelve rows of secondary wood radiating out from the central triangular protostele. Note that interfascicular and fascicular wood are identical towards outer margin. Ray structure uniform throughout. From slide 1532, × 11.

Fig. 12. Transverse section of a portion of stem showing interfascicular wood, cambium and two layers of periderm: *a*, inner periderm. From slide 1533, × 22.

Fig. 13. Longitudinal-tangential view of secondary wood: *a*, horizontal-radiate ray approximately six cells deep. From slide 1534, × 60.

Explanation of Plate

PLATE 14

Sphenophyllum plurifoliatum

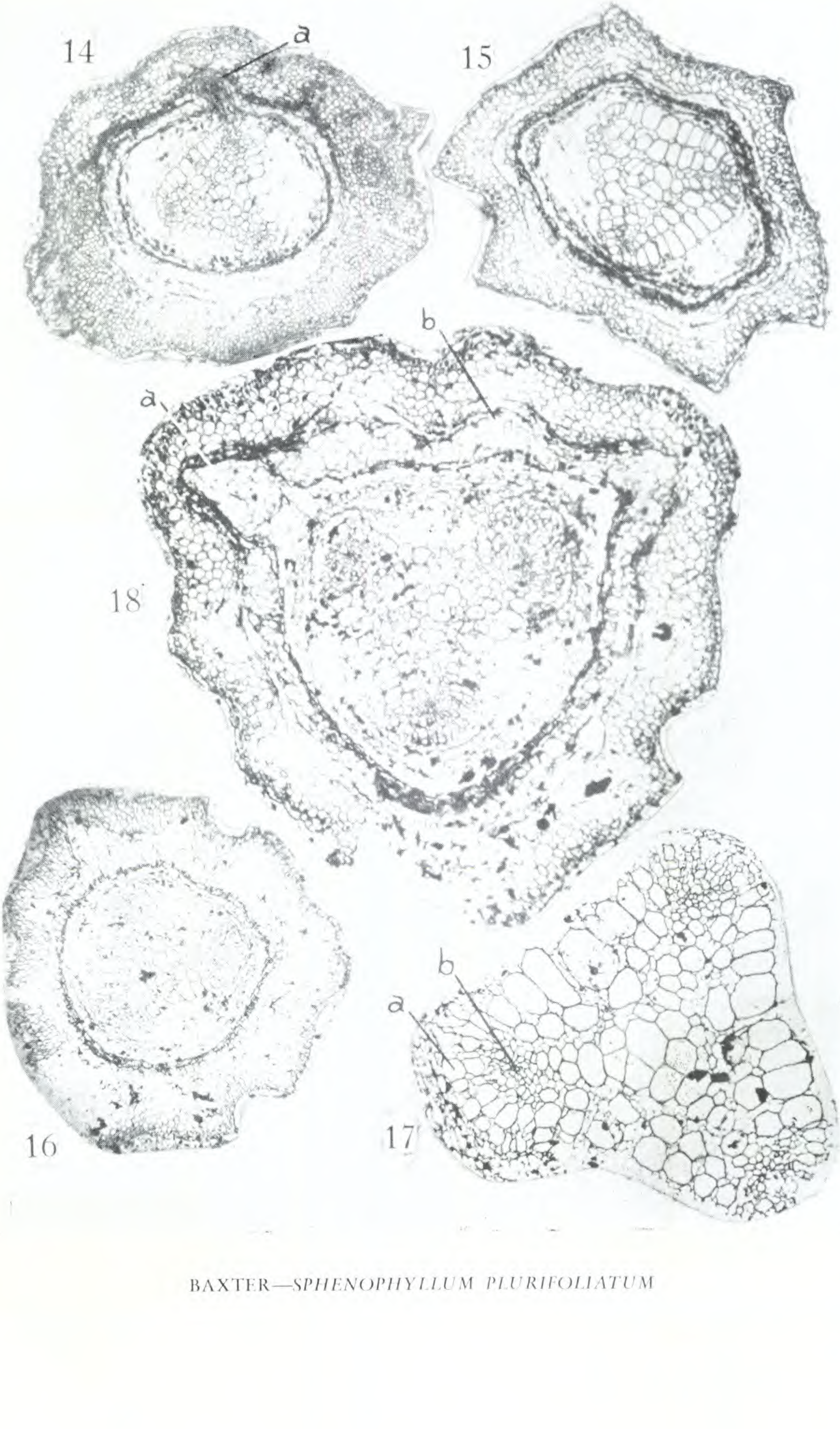
Fig. 14. Transverse section of stem in region of the internode showing production of adventitious root: *a*, adventitious root arising from protoxylem. From slide 1535, × 18.

Fig. 15. Transverse section of same stem as in fig. 14 showing characteristic hexagonal shape. From slide 1536, × 18.

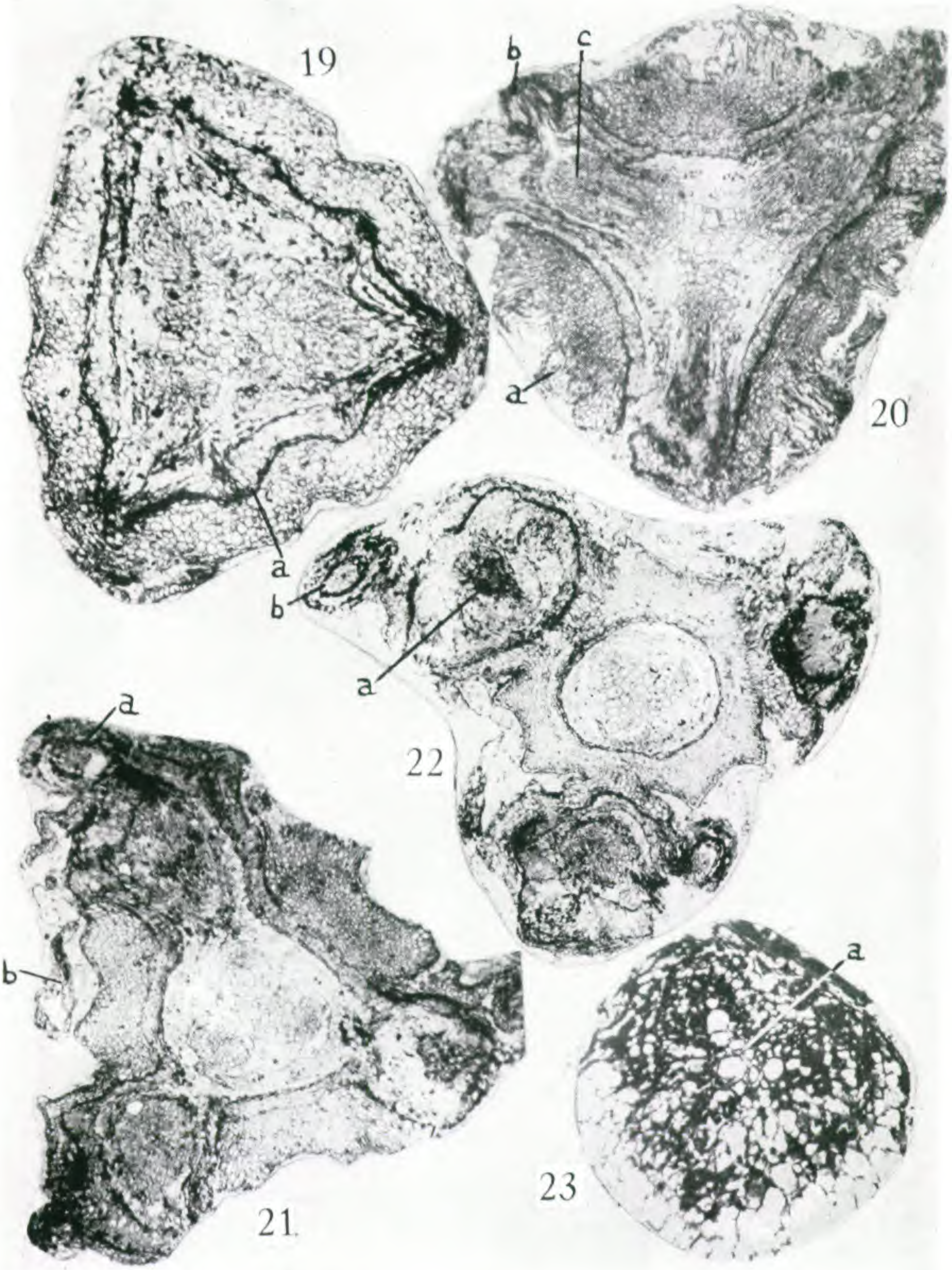
Fig. 16. Same stem as above, with section approaching the node. Note rounded outline and clearly defined cortical furrows opposite interfascicular wood. From slide 1537, × 18.

Fig. 17. Enlargement of the stele of preceding figure: *a*, secondary wood; *b*, protoxylem. From slide 1537, × 60.

Fig. 18. Same stem as above, transverse section at lower edge of the node: *a*, adventitious root preceding branch; *b*, swelling in periderm at position of trace to a side leaf. From slide 1538, × 24.



BAXTER—*SPHENOPHYLLUM PLURIFOLIATUM*



BAXTER—*SPHENOPHYLLUM PLURIFOLIATUM*

Explanation of Plate

PLATE 15

Sphenophyllum plurifoliatum

Fig. 19. Same stem as in fig. 18, showing a section slightly nearer the center of the node: *a*, trace to one of six side leaves. From slide 1539, × 12.

Fig. 20. Continuing nodal series in same stem: *a*, leaf base of one of six side leaves; *b*, adventitious root; *c*, vascular bundle to branch. From slide 1537, × 12.

Fig. 21. Same stem as above; vascular bundles to branches have become separated from main stele: *a*, adventitious root shown in fig. 20 *(b)*: *b*, segment of one of six side leaves. From slide 1540, × 12.

Fig. 22. Continuing nodal series in same stem, showing whorl of three branches almost free from the main stem: *a*, triangular primary wood; *b*, adventitious root. From slide 1541, × 12.

Fig. 23. Enlargement of central portion of one of the three branches at a slightly higher point: *a*, triangular protostele. From slide 1542, × 75.

Explanation of Plate

PLATE 16

Sphenophyllum plurifoliatum

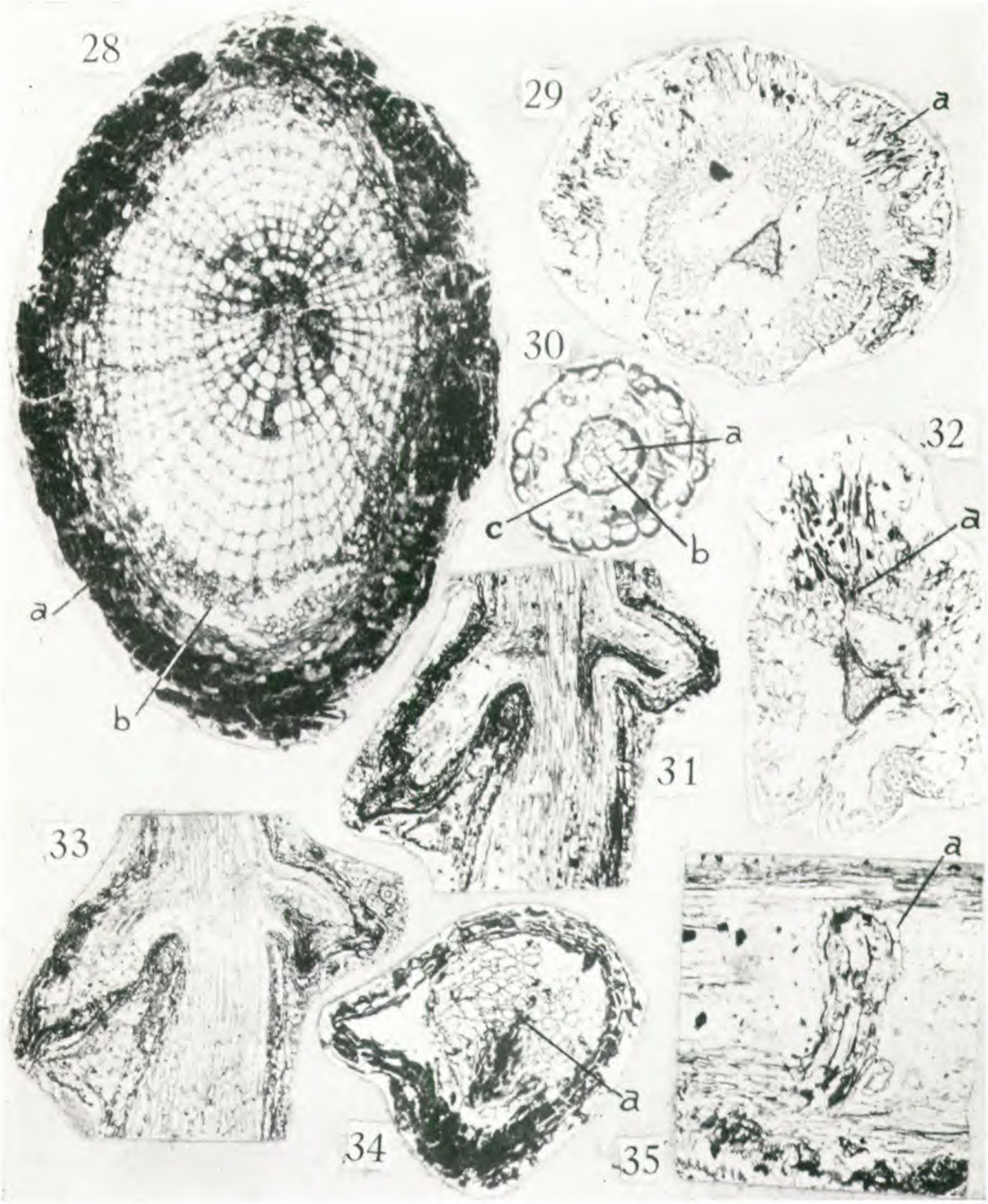
Fig. 24. Segment of a *Sphenophyllum* leaf showing conspicuous dark fiber ring surrounding small elements of vein. From slide 1543, × 120.

Fig. 25. Transverse section of a stem showing branching: *a*, root branching; *b*, modified adventitious root; *c*, large bundle of fascicular wood coming off into side branch. From slide 1544, × 22.

Fig. 26. Same stem as in fig. 25 at higher point of branch departure: *a*, vascular bundle shown in fig. 25 *(c)* now separated from the central stele. From slide 1545, × 22.

Fig. 27. Transverse section of a small stem at a node with portions of its six leaves surrounding it. From slide 1546, × 26.

BAXTER—*SPHENOPHYLLUM PLURIFOLIATUM*



BAXTER—*SPHENOPHYLLUM PLURIFOLIATUM*

Explanation of Plate

PLATE 17

Sphenophyllum plurifoliatum

Fig. 28. Transverse section of a large root: *a*, periderm; *b*, phloem. From slide 1547, × 20.

Fig. 29. Transverse section of a stem at a node showing fused whorl of leaves: *a*, leaf base. From slide 1546, × 24.

Fig. 30. Transverse section of a small root: *a*, secondary xylem; *b*, protoxylem; *c*, endodermis. From slide 1526, × 45.

Fig. 31. Longitudinal section of a stem with large branching roots. Note horizontal passage of vascular tissue into right-hand root. From slide 1548, × 15.

Fig. 32. Transverse section of a small stem at node: *a*, V-shaped leaf traces shown pulled away from the protoxylem angle of the stele. From slide 1546, × 24.

Fig. 33. Same stem as in fig. 31, showing branching of small roots from one of the large roots. From slide 1534, × 15.

Fig. 34. Transverse section of small root showing endogenous origin of branch root: *a*, protoxylem. From slide 1549, × 30.

Fig. 35. Longitudinal section through the middle cortex of a stem showing an adventitious root in both transverse and longitudinal view: *a*, characteristic large epidermal cells. From slide 1550, × 23.

MISCELLANEOUS NEW APOCYNACEAE AND ASCLEPIADACEAE

ROBERT E. WOODSON, JR.

Morleya Woodson, gen. nov. Apocynacearum (Plumerioideae-Plumerieae-Alstoniinae).—Calyx 5-partitus eglanduligerus, lobis aequalibus imbricatis in anthesim caducis. Corolla salverformis, tubo ampulliformi basi staminigero, limbi lobis 5 aestivatione sinistrorso. Antherae 5 subsessiles omnino fertiles compresse ovatae. Ovarii carpella 2 valde subinferiora super receptaculo apocarpa, ovulis in quoque loculo ca. 16, 4-seriatim positis, stigmate sessili doliiformi apiculis 2 minutis erectis minute puberulo-papillatis, nectario nullo. Fructus ignotus.—Arbores. Folia alternata, petiolo supra medio glanduligero. Inflorescentia terminalis thyrsiformis pluriflora, bracteis minimis. Species typicum succedit:

MORLEYA **leipocalyx** Woodson, spec. nov.—Arbor ca. 12 m. alta, ramulis teretibus glabris cortice brunneis. Folia petiolata oblonga vel obovato-oblonga apice valde acuminata basi abrupte decurrentia cum petiolo ad medio glanduligero 10–12 cm. longa 2–3 cm. lata firmiter membranacea glabra. Inflorescentia glabra ramosa foliis brevior, pedicellis ca. 0.5 cm. longis, bracteis minimis caducis. Calycis laciniae ovato-trigonales ca. 0.1 cm. longae minute ciliolatae mox caducae. Corollae albae extus glabrae tubus ampulliformis ca. 1.3 cm. longus basi ca. 0.1 cm. diam. ibique staminiger lobi oblongo-dolabriformes ca. 1.4 cm. longi 0.6 cm. lati patuli. Antherae ca. 0.15 cm. longae. Ovarii carpella glabra vix 0.1 cm. alta; stigmate ca. 0.1 cm. alto. Nomen e *λειπο* et *κάλυξ* compositum. —COSTA RICA: Guanacaste: near ridge crest, alt. ca. 200 m.; north of La Cruz on proposed route of Inter-American Highway, 14 miles south of Nicaraguan border, Aug. 13, 1946, *Thomas Morley 770* (Herb. Chicago Nat. Hist. Mus., TYPE).

Morleya suggests relationship to *Plumeria* through its half-inferior ovary, but is distinguished amongst all known Alstoniinae through its peculiar caducous calyx lobes and glandular petioles. I am indebted to Dr. P. C. Standley for calling my attention to this remarkable plant.

MANDEVILLA **longipes** Woodson, spec. nov.—Frutex volubilis ca. 5–7 m. altus ramulis tenuibus ferrugine hirtellis internodiis sat elongatis. Folia opposita petiolata elliptica apice subcaudato-acuminata basi anguste sagittato-cordata 6–9 cm. longa 2–4 cm. lata utrinque puberulo-hirtella supra nervo medio sparse glanduligero petiolo 0.5–1.0 cm. longo. Inflorescentiae axillares alternatae racemiformes pluriflorae pedunculo 8–10 cm. longo sparse minuteque hirtello bracteis lanceolatis 0.2–0.3 cm. longis. Flores ut dicuntur albi medio fulvi; pedicellis elongatis tenuibus 2.0–2.5 cm. longis minute hirtellis; calycis laciniis ovatis acutis ca. 0.2 cm. longis; corollae salverformis vel subsalverformis tubo ca. 3 cm. longo basi ca. 0.1 cm. diam. ostio ca. 0.2 cm. diam. indistincte gibboso paullo supra medio staminigero lobis dolabriformibus ca. 1.5 cm. longis patulis valde contortis. Folliculi valde moniliformes tenues 15–20 cm. longi laeves.—COLOMBIA: BOYACA:

[1] Issued September 20, 1948.

low thin forest, alt. 4500 ft., La Chapon, July 27, 1932, *A. E. Lawrance 361* (Herb. Missouri Bot. Gard., TYPE). At first mistaken for *M. subsagittata*, to which it must be closely related, but differing in its conspicuously elongate, lax (not secund) pedicels. In addition, the flower color of the latter species, as I know it in Panama, is a soft yellow, but with the "brownish yellow center" of which Mr. Lawrance speaks (or possibly more nearly reddish-orange).

MANDEVILLA **turgida** Woodson, spec. nov.—Suffrutex ut videtur suberecta habitu ignota; ramulis crassiusculis cortice irregulariter subalatis rubro-brunneis minute puberulis internodiis ca. 1.0–1.5 cm. longis; foliis oppositis breviter petiolatis ellipticis vel oblongo-ellipticis apice basique acutis 3–4 cm. longis 1.0–1.7 cm. latis rigide coriaceis subenervis illustribus nervo medio supra ad longitudinem sparse glanduligero subtus minute puberulis caeterumque glabris petiolo ca. 0.3 cm. longo; inflorescentiae racemiformes subterminales pluriflores pedunculo ca. 1.5 cm. longo; pedicellis ca. 0.3 cm. longis minute puberulis; bracteis scariaceis minimis; calycis laciniis ovato-lanceolatis anguste acutis ca. 0.15 cm. longis papillatis, intus basi multiglanduligeris; corollae infundibuliformis gilvae extus glabrae tubo proprio ca. 1.5 cm. longo basi ca. 0.15 cm. diam. faucibus anguste campanulatis ca. 1.7 cm. longis ostio ca. 1 cm. diam. lobis oblique obovatis breviter apiculatis ca. 1 cm. longis patulis; antheris oblongo-sagittatis dorso glabris ca. 0.4 cm. longis basi truncate 2-lobatis; carpellis oblongoideis ca. 0.15 cm. longis glabris; nectariis 5 plus minusve concrescentibus ovaria ca. dimidio aequantibus; stigmate umbraculiformi breviter apiculato ca. 0.2 cm. longo; folliculis ignotis. —VENEZUELA: BOLIVAR: Cerro Guaiquinima, Alto Río Paragua, alt. 1740 m., Oct., 1943, *F. Cardona 959* (U. S. Nat. Herb., TYPE).

A most unusual member of the shrubby section of subgen. Exothostemon; allied to the *M. Vanheurckii* complex, of which the old Roraima Shield so abounds, but differing from all in the extremely small, elliptic leaves.

MALOUETIA **Quadricasarum** Woodson, spec. nov.—Arbor ca. 15 m. alta trunco basi ca. 20 cm. diam. Ramuli dichotomi glabri cortice brunneo. Folia opposita lamina late elliptica apice longiuscule subcaudato-acuminata basi late obtusa 10–15 cm. longa 5.0–6.5 cm. lata subcoriacea glabra. Cymae umbelliformes subsessiles pluriflorae. Flores albo-galbini; pedicello ca. 1 cm. longo glabro; calycis laciniis subfoliaceis haud imbricatis apicem versus patulis oblongo-lanceolatis apice obtusis vel rotundatis 0.3–0.35 cm. longis margine sparse ciliatis caeterumque glabris intus basi ad margines 1-squamelligeris; corollae salverformis tubo anguste conico ca. 1.2 cm. longo basi ca. 0.12 cm. diam. ostio ca. 0.05 cm. diam. faucibus staminigeris ibique callosis 5-dentatis extus omnino glabro, lobis patulis inaequilateraliter elliptico-lanceolatis ca. 1 cm. longis extus glabris intus dense pilosis; antheris exsertis ca. 0.25 cm. longis dorso dense pilosis; ovario ca. 0.15 cm. alto dense piloso, nectario annulari; stigmate fusiformi ca. 0.1 cm. longo. —COLOMBIA: El Valle: costa del Pacifico, Río Cajambre, Silva, alt. 5–80 m., May 5–15, 1944, *J. Cuatrecasas 17522* (Herb. Missouri Bot. Gard., TYPE).

In my revision of *Malouetia* (Ann. Missouri Bot. Gard. 22:238. 1935), this species keys to the neighborhood of *M. Schomburgkii* because of its subfoliaceous calyx lobes, although its general appearance is more suggestive of the widespread *A. tamaquarina*.

PRESTONIA **Haughtii** Woodson, spec. nov.—Suffrutex volubilis alte scandens; ramulis crassiusculis glabris bene lenticellatis. Folia opposita breviter petiolata lamina obovato-ovali apice mucronulata basi obtusa vel late acuta 20–30 cm. longa 8–11 cm. lata firmiter membranacea vel subcoriacea glabra supra illustri subtus pallidiori petiolo ca. 1 cm. longo. Inflorescentia terminalis simplex racemiformis ca. 15-flora pedunculo deflexo ca. 8–10 cm. longo glabro bracteis minimis. Flores apicem versus subaggregati; pedicello ca. 1.5 cm. longo inconspicue pilosulo; calycis campanulati coriacei ut videtur plus minusve purpurissati ca. 1.5 cm. longi laciniis ovato-trigonalibus acutis ca. 1 cm. longis indistincte papillatis intus squamellam deltoideam minute erosam instructis; corollae salverformis pallide luteae tubo cylindrico ca. 1.5 cm. longo basi ca. 2 mm. diam. extus glabro, lobis late dolabriformibus ca. 1 cm. longis patentibus, faucium annulo ca. 2 mm. alto obscure 5-lobato albo, appendicibus epistaminalibus vix inclusis ca. 1 mm. longis; antheris vix inclusis ca. 5 mm. longis valde sagittatis glabris; ovariis ca. 1 mm. longis glabris, stigmate non viso, nectariis 5 carnosis basi concrescentibus ca. 2.5 mm. longis. Folliculi ignoti.—COLOMBIA: ANTIOQUIA: edge of forest, alt. under 50 m., Nicocli, June 25, 1946, O. *Haught 4911* (Herb. Missouri Bot. Gard., TYPE).

Closely allied to the following, but differing in the more elongate leaves, somewhat shorter corolla-tube, and nectaries surpassing the ovary.

PRESTONIA **macrophylla** Woodson, spec. nov.—Suffrutex volubilis alte scandens; ramulis crassiusculis glabris valde longitudinaliter striatis et inconspicue lenticellatis. Folia opposita breviuscule petiolata; lamina late obovata apice emarginata basi obtusa vel latissime acuta coriacea glabra supra illustri subtus pallidiori; petiolo ca. 1 cm. longo. Inflorescentia terminalis simplex racemiformis ca. 20-flora; pedunculo 8–10 cm. longo; bracteis minimis. Flores haud specialiter aggregati spiraliter dispositi; pedicello ca. 1 cm. longo sparse appresse pilosulo; calycis basi campanulati coriacei ut videtur plus minusve purpurissati ca. 1.5 cm. longi laciniis oblongo-trigonalibus acuminatis ca. 7 mm. longis extus sparse appresseque pilosulis squamellam 3-angularem ca. 3 mm. longam munitis; corollae salverformis pallide luteae tubo ca. 2 cm. longo basi ca. 4 mm. diam. apicem prope paulo attenuato extus glabro, lobis late dolabriformibus ca. 2.5 cm. longis patulis, faucium annulo ca. 3 mm. alto obscure 3-lobato, appendicibus epistaminalibus inclusis linearibus ca. 3 mm. longis; antheris vix inclusis valde sagittatis 5 mm. longis glabris; ovariis ovoideis glabris ca. 1 mm. longis; nectariis 5 carnosis basi coalitis ca. 2 mm. longis. Folliculi ignoti.—COLOMBIA: ANTIOQUIA: Río Turbo at mouth of Quebrada de los Indios, alt. under 50 m., Turbo, July 15, 1946, O. *Haught 4377* (Herb. Missouri Bot. Gard., TYPE).

At first sight, this species may be mistaken for *P. obovata*, of Panama, from which it differs in the fleshy texture of the floral nectary, typical of the South American representation of the § Annulares. Actually, the closest relative of *P. macrophylla* appears to be the preceding species and *P. didyma*, from which it differs in the obovate leaves, minute bracts, and larger flowers.

FORSTERONIA **propinqua** Woodson, spec. nov.—Suffrutex volubilis gracilis; ramulis gracilibus bene lenticellatis glabratis juventate ferrugineo-pilosulis. Folia opposita breviter petiolata lamina elliptico-oblonga anguste acuminata basi obscurissime cordata 5–8 cm. longa 2–3 cm. lata delicate membranacea opaca supra glabra subtus in axillis nervi medii ferrugineo-barbata nervo medio supra basi pauciglanduligero, petiolo 3–4 mm. longo. Inflorescentia terminalis spicate thyrsiformis multiflora; pedunculo ca. 4–5 cm. longo; pedicellis subnullis. Calycis laciniae ovatae acutae ca. 2 mm. longae extus minute pilosulae esquamelligerae. Corollae rotato-campanulatae extus glabrae gilvae tubus ca. 1 mm. longus faucibus ca. equilatis; lobis ovato-oblongis ca. 2.5 mm. longis patulis; antheris valde exsertis oblongo-panduliformibus basi 2-lobatis ca. 1.5 mm. longis glabris; ovario syncarpo ca. 0.5 mm. longo pilosulo; stigmate umbraculiformi ca. 1.5 mm. longo longe 2-apiculato; nectariis 5 discretis ovarium semiaequantibus. Folliculi ignoti.—COLOMBIA: ANTIOQUIA: forest on Río Guadualito, alt. about 50 m., Turbo, May 1, 1946, *O. Haught 4818* (Herb. Missouri Bot. Gard., TYPE).

This species is remarkable in its syncarpous ovary, which allies it with *F. spicata* of the Caribbean basin of Central and South America and the Antilles, a very common species. From that species, *F. propinqua* may be separated readily by the smaller, oblong-elliptic foliage and strictly terminal inflorescences which are less densely pubescent and with somewhat smaller flowers.

FORSTERONIA **mediocris** Woodson, spec. nov.—Frutex volubilis, ramulis graciliusculis conspicue lenticellatis glabris internodiis sat elongatis. Folia opposita petiolata elliptico-oblonga apice breviuscule subcaudato-acuminata basi rotundata 10–12 cm. longa 4.5–5.5 cm. lata membranacea utrinque glabra, petiolis ca. 0.7 cm. longis. Inflorescentia terminalis anguste thyrsiformis multiflora, pedunculo primario ca. 12 cm. longo minutissime puberulo-papillato ramulis secundariis pluribus basi ca. 2.5 cm. apicem versus gradatim abbreviatis usque 0.1 cm. longis puberulo-papillatis, pedicellis congestis ca. 0.1 cm. longis ut in pedunculis vestitis, bracteis minutis vix bene visis; calycis laciniis late deltoideis acutis 0.1 cm. longis extus minute puberulo-papillatis squamellis nullis; corolla alba campanulata extus intusque minute puberulo-papillata tubo ca. 0.05 mm. longo lobis patulis ovato-ellipticis ca. 0.15 cm. longis; antheris fere plane exsertis 0.08 cm. longis apice pilosulis basi truncatis vix 2-lobatis filamentis liberis; ovario apocarpo ca. 0.05 mm. alto minute pilosulo stigmate incluso ca. 0.05 cm. alto, nectariis 5 integris ovarium aequantibus.—COLOMBIA: CAQUETA: Florencia, entre matorrales residuales de monte, alt. 400 m., Marzo 29, 1940, *J. Cuatrecasas 8800* (U. S. Nat. Herb., TYPE).

This species, the general appearance of which is conveyed by the specific adjective, apparently is closely allied to *F. elachista* Blake and *F. graciloides* Woods., both of which have more diffuse, floriferous inflorescences and roughly obovate leaves; in *F. mediocris*, as well, the flowers are somewhat larger, and the larger anthers more widely exserted.

MATELEA **purpureolineata** Woodson, spec. nov.—Herbae volubiles fere omnino parte trifariam pubescentes pilis et laxe strigulosis et densius minuteque puberulis tum glandularibus tum eglandularibus; ramulis gracilibus internodiis elongatis. Folia opposita longe petiolata ovato-elliptica acuminata cordata sinu lato lobis inflexis 3.5–5.5 cm. longa 2–3 cm. lata membranacea; petiolis tenuibus 2.0–2.5 cm. longis. Inflorescentia alternato-axillaris corymbiformis pluriflora; pedunculo ca. 1 cm. longo; pedicellis ca. 0.5 cm. longis; bracteis minutis. Calycis lobi 5 oblongo-ovati acuminati ca. 0.4 cm. longi extus trifariam pubescentes, squamellis alternatis solitariis ovoideis compressis. Corolla rotato-campanulata gilva venulis 15 purpureis ornata extus pubescens; tubo ca. 0.45 cm. longo ostio ca. 0.3 cm. diam. intus sparse pilosulo prope mediam staminigero; lobis late oblongo-ellipticis apice rotundatis paululo obliquis patulis ca. 0.7 cm. longis. Gynostegium subsessile tubi corollae prope mediam insertum ca. 0.15 cm. diam.; stigmate late umbonato; polliniis horizontalibus latissime reniformibus inaequaliter compressis ca. 0.25 mm. longis, caudiculis subnullis, corpusculo anguste sagittato minuto. Corona annulata lobis 5 latissime 3-angularibus patulis ca. 0.25 mm. longis quibusque processu interiore anguste ligulato ca. 1.25 mm. longo supra gynostegium alte inflexo. Folliculi ignoti.—COLOMBIA: CUNDINAMARCA: hillside east of Apulo, along trail to Anapoima, alt. 460–600 m., thickets, May 4, 1944, *E. P. Killip, A. Dugand & R. Jaramillo 38165* (Herb. Missouri Bot. Gard., TYPE; U. S. Nat. Herb., ISOTYPE).

This species, referable to subgen. *Chthamalia* (cf. Ann. Missouri Bot. Gard. 28:221. 1941), is particularly notable amongst the Mateleas known to me because of the long, narrow, inflexed internal processes of the corona lobes, and the high insertion of the gynostegium, recalling *Gonolobus* subgen. *Pseudolachnostoma*.

A NEW AMSONIA FROM THE TRANS-PECOS

AMSONIA **Tharpii** Woodson, spec. nov.—Herbae perennes suffrutescentes caudice lignoso inveterato ramis herbaceis pluribus 1–2 dm. altis densiuscule canescenti-pilosis. Folia alternato-approximata congesta subsessilia anguste lanceolata acuminata 2.5–4.0 cm. longa 0.2–0.35 cm. lata rarius basi latiuscule elliptica usque 1.2 cm. lata subcoriacea glabra vel nervo medio inferne sparse pilosulo. Inflorescentia terminalis pauciflora. Flores mediocres ut videntur dilute caerulei pedicellis pilosulis ca. 0.3 cm. longis. Calycis laciniae anguste lanceolatae longe acuminatae ca. 0.35 cm. longae subfoliaceae apicem versus pilosulo-barbatae. Corollae subsalverformis extus omnino glabrae tubus 1.4 cm. longus basi ca. 0.1 cm. diam. faucibus intus pilosulis ca. 0.2 cm. diam. lobis anguste ellipticis ca. 0.6 cm. longis patulis. Stamina prope corollae fauces inserta antheris 0.2 cm. longis.

Ovaria oblongoidea glabra ca. 0.15 cm. alta stylo gracili stigmate globoso papillato ca. 0.1 cm. diam. apice obtuse 2-lobato. Folliculi breviusculi crassiusculi subfusiformes continui glabri ca. 2.5–3.5 cm. longi.—TEXAS: PECOS: frequent on limestone hills 21 miles northeast of Ft. Stockton, on McCamey highway, April 19, 1946, *B. H. Warnock 46183* (Herb. Missouri Bot. Gard., TYPE; Herb. Univ. Texas, ISOTYPE); mesa remnant with guayule, June 21, 1943, *B. C. Tharp 43-508* (Herb. Missouri Bot. Gard.; Herb. Univ. Texas).

This rather unattractive, but wholly distinctive, species was first sent to me in the fruiting condition by Dr. Tharp in 1943. Failing to recognize it, I suggested that a look-out for it be kept upon future visits to Pecos County. This spring Mr. Warnock came upon it apparently in considerable numbers and in good flowering condition. Upon first glance at the flowers, I was disgusted to see how closely they resemble those of such ambiguous species as *A. Palmeri*, *A. hirtella* and *A. Peeblesii* in a superficial way. Then, with my specimens of the last-named species before me, I noticed that in all of them the stamens are inserted slightly above midway within the corolla-tube, whilst in Mr. Warnock's plant the stamens are inserted in the upper quarter of the tube, close beneath the orifice. This difference in position of the stamens results in a slightly different constriction of the corolla orifice, as well as corolla throats of somewhat different shape, the throat of *A. Tharpii* being decidedly shorter and more abruptly constricted than in the neighboring species. Thus, I have no further qualms about the description of the novelty, and am pleased to dedicate it to Dr. Tharp who richly merits such recognition. The woody caudex of the type specimen of *A. Tharpii* is very strikingly thickened and lignified, appearing like a dwarfed Japanese tree ("bonsai") with the many stem-bases of past seasons. It must be many years old.

QUANTITATIVE DETERMINATION OF THE PIGMENT CONTENT OF SINGLE CELLS BY MEANS OF A NEW MICROSPECTROPHOTOMETER

BARRY COMMONER

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I. Introduction

Information concerning the physiological activities of single living cells has long been a goal of biological investigation. Analytical biochemistry of tissue masses, while yielding precise chemical data, unfortunately is limited by the fact that it involves procedures tending to disrupt the integrated chemical activities which are the mark of living cells. On the other hand, integrated information can be obtained from studies of whole organisms, organs or tissue fragments, but the data necessarily represent a pooling of the varied rates and directions of chemical activities of at least many thousands of cells.

It has become increasingly clear that these classical methods need to be supplemented by procedures which can produce data referable to individual cells. Thus, for example, investigation of the mechanisms involved in the enormously varied biochemical expression of presumably identical nuclei in the different cells of an organism demands data which can distinguish between biochemical activities of two neighboring cells in a tissue.

Almost the only means of investigating single tissue cells—without removing them from their neighbors and injuring them to the point of death—is light. Because many of the cellular compounds of interest to the biologist have rather characteristic absorption spectra, the determination of the optical density of a living cell in light of various wave-lengths can supply data on the type and amount of certain of these substances present. Since the pioneer investigations of MacMunn (1914), spectroscopy has attracted increasing interest as a means of probing the living cell. Quantitative studies of cellular absorption spectra became possible when several German optical firms developed photographic spectrographs for use with high-power microscopes (see Dhéré, 1933). More recently modern photoelectrical methods have been applied to this type of apparatus by the school of Caspersson (1940) in Sweden, and by Pollister and Ris (1947) in this country. Their work, while chiefly concerned with the determination of nucleic acids and proteins in various parts of the cell, has shown conclusively that microspectrophotometry is technically sound (with proper precautions) and admirably suited to the development of new methods for studying single cell physiology.

The present paper describes a new microspectrophotometer, designed specifically for the study of the biochemical changes which occur in single living cells. As an example of its applicability to this problem, studies of the pigment content of single plant cells are also presented.

II. The Apparatus

The equipment is diagrammed in fig. 1. To simplify the problem of providing a source of monochromatic light throughout the spectrum, a Beckman quartz spectrophotometer is used as a source. This instrument, with its photocell housing and cell-carrier removed, is positioned to direct its light-beam into a vertical microscope. In place of the usual movable substage microscope mirror, a fixed 45-degree first-surface aluminized mirror is mounted on the microscope base to direct the light into the microscope. The microscope and spectrophotometer are rigidly mounted on a common base. To permit the use of the Beckman instrument in its own capacity, the latter is mounted on a sliding track so that it can be moved away from the microscope.

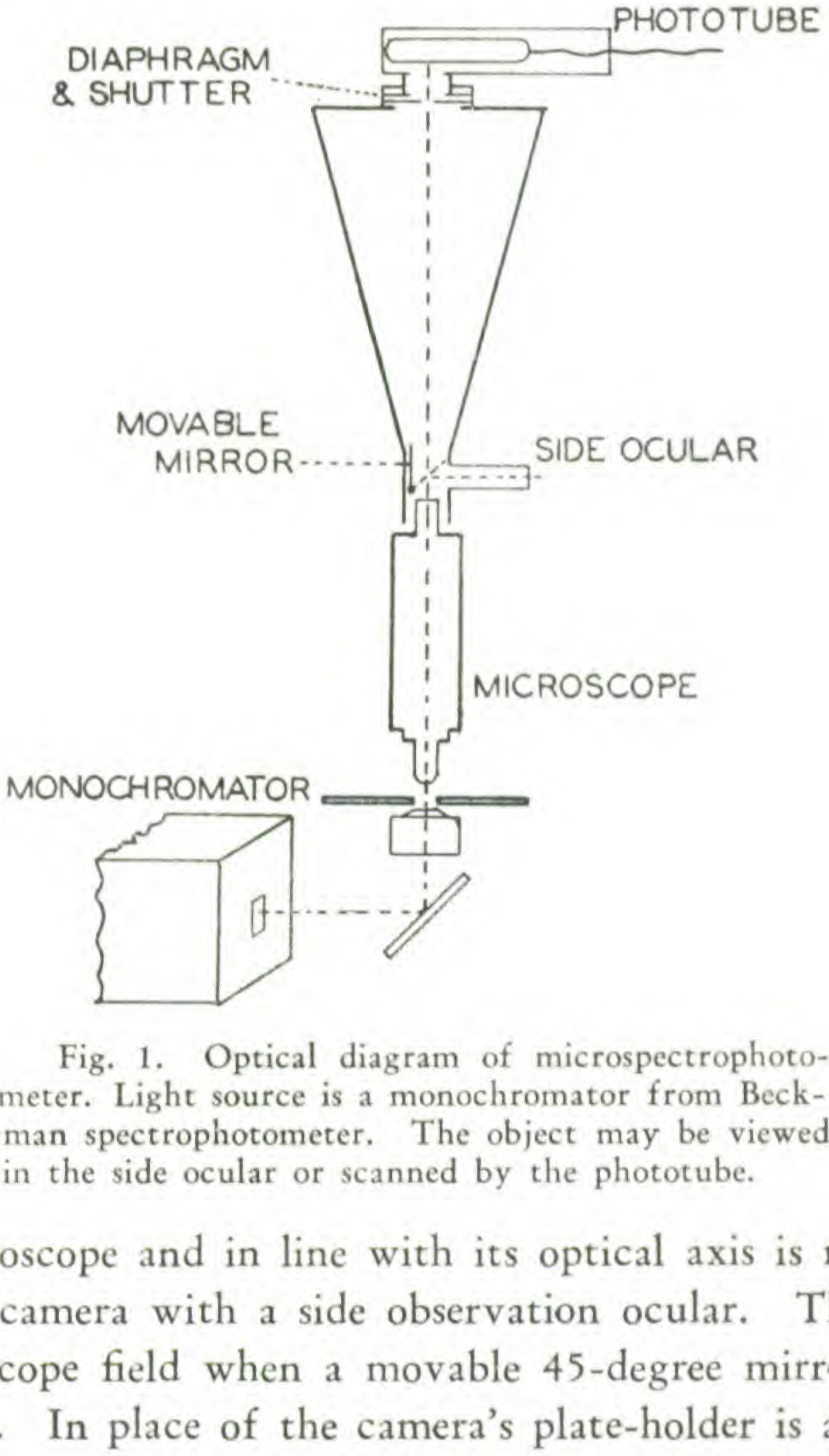

Fig. 1. Optical diagram of microspectrophotometer. Light source is a monochromator from Beckman spectrophotometer. The object may be viewed in the side ocular or scanned by the phototube.

Above the microscope and in line with its optical axis is mounted a modified photomicrographic camera with a side observation ocular. The latter provides a view of the microscope field when a movable 45-degree mirror is thrown across the microscope axis. In place of the camera's plate-holder is a board on which is fastened a large camera shutter and iris diaphragm. The latter is used to determine the area of the image scanned by the photocell, which is mounted directly into the shutter frame. The photocell is of the photomultiplier type, and is used in conjunction with a Photovolt amplifier.

The microscope is equipped with a set of apochromatic lenses and a condenser of N.A. 1.4. The emergent beam of the Beckman instrument is well collimated,

and by proper focusing of the substage condenser critical illumination can be attained. The side observation ocular contains a cross-hair and ocular micrometer. The entire apparatus is aligned so that the object centered in the cross-hair is also centered in the opening of the diaphragm below the photocell. The ocular is further adjusted to bring the object into sharp focus when its image lies in the plane of the photocell. In this way it is possible to select by the side ocular the precise area to be scanned by the photocell. By rotating the ocular mirror, the light path can then proceed to the photocell and the measurement can be made.

The instrument is operated as follows: The wave-length dial of the spectrophotometer is set at the desired wave-length. The object is brought into view in the side ocular and the size of the area to be studied is determined on the ocular scale. The upper diaphragm is then set to this size. The slide is moved slightly so that the cross-hairs fall on a clear area just next to the object (mounted in water). The mirror is then thrown out of position and the apparatus adjusted to yield a full-scale deflection on the photocell galvanometer. This can be done by altering either the slit-width of the spectrophotometer, the opening of the substage diaphragm (within small limits), or the sensitivity of the amplifier. The ocular mirror is brought into position again and the slide moved to bring the desired area of the study object into the cross-hair point. The mirror is immediately thrown out again. The galvanometer then reads the transmission of the object as per cent of the incident light which emerges. The procedure is then repeated at a new wave-length and so on until the desired spectral range has been examined. In practice it is possible to make a single reading in about 30–40 seconds.

The equipment functions within the range 340–800 mμ, and its lower limit is due only to the lack of quartz optics in the microscope. A minimum object area of 4 μ can be studied. The amount of light incident on the object area is so small that no heat damage has been observed. *Tradescantia* staminal hair cells, for example, continue to show active protoplasmic streaming at the end of the determination of a complete absorption spectrum.

III. Optical Accuracy

The entire apparatus was tested for optical accuracy by determining the absorption spectrum of a sample of crystalline cyanin in 1 per cent HCl (concentration: 6.64 mgm. per liter). The solution was placed in a quartz micro-absorption cell, 1 cm. thick, and a matched cell was filled with pure solvent. Both cells were sealed and placed side by side (on a clean slide) on the microscope stage with their optical faces horizontal. The 40$\times$ objective was focused on the upper surface of the solvent cell, and the stage coordinates noted. A corresponding position for the test cell was also determined and coordinates noted. The transmission of the sample was then determined by setting the galvanometer scale to 100 with the solvent in focus and then moving to the noted area of the sample cell. In this way the absorption spectrum of the cyanin sample was obtained in the region of its characteristic visible absorption band. This completed, the cells were removed

from the glass slide and placed in the regular Beckman cell carrier in the usual way. The spectrophotometer was reassembled and the absorption spectrum of the sample redetermined in the Beckman instrument itself.

The two sets of data obtained from the same sample are presented in fig. 2. It will be noted that the spectral agreement is complete, the sample yielding its characteristic absorption peak of 510 mμ on both instruments. Thus the microspectrophotometer seems to be accurate with regard to the spectral bands which impinge on the object at various positions of the Beckman wave-length scale. Furthermore, it will be noted that the optical density of the sample at its absorption peak is

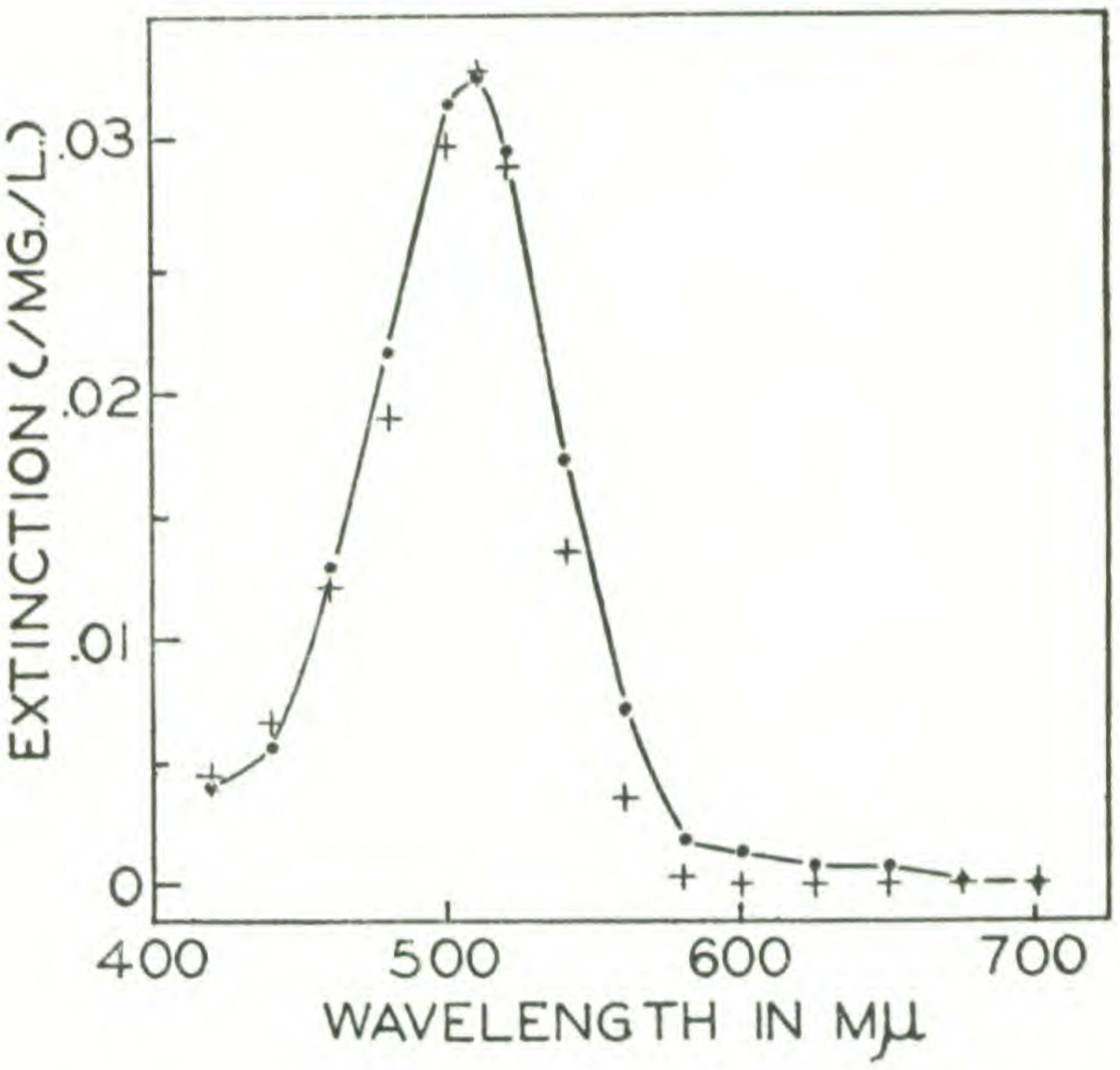

Fig. 2. Absorption spectra of the same sample of cyanin (6.64 mg. per liter in 1 0/0 HCl) obtained by the microspectrophotometer (solid line) and a Beckman spectrophotometer (points indicated by +).

practically identical for both sets of data (extinction = .317 on the microspectrophotometer; extinction = .318 on the Beckman instrument). This indicates that the apparatus is accurate with regard to intensity measurements, and that its response is adequately linear. It will be noted that there is a small discrepancy between the two absorption spectra at the limits of the cyanin band. This may be due to the fact that the slit widths used in the micro determination (1.0–2.0 mm.) were twice those used on the Beckman instrument. This was necessitated by the excessive light loss caused by the thick cell and does not occur in ordinary measurements which can be made at slit widths of .1–.7 mm.

IV. Determination of Pigments in Single Coleus Hair-cells

Coleus is a convenient plant for the study of the physiology of pigment production. Its many varieties produce a very wide range of anthocyanin concentrations, and cells of varying degrees of pigmentation frequently can be obtained from the same plant. The studies reported below were initiated as a preliminary step in the investigation of the biochemical effects of virus infections which produce strong alterations in the degree of pigmentation of *Coleus*.

Pigment production in this plant is chiefly localized in the epidermal cells of the leaves. Of these cells, those comprising the hairs covering the leaf's upper surface are best suited to optical measurements. Because of their regular shape (truncated cones), the thickness of any given part of such a cell can be determined by measuring its diameter at that point. The regular shape also permits easy

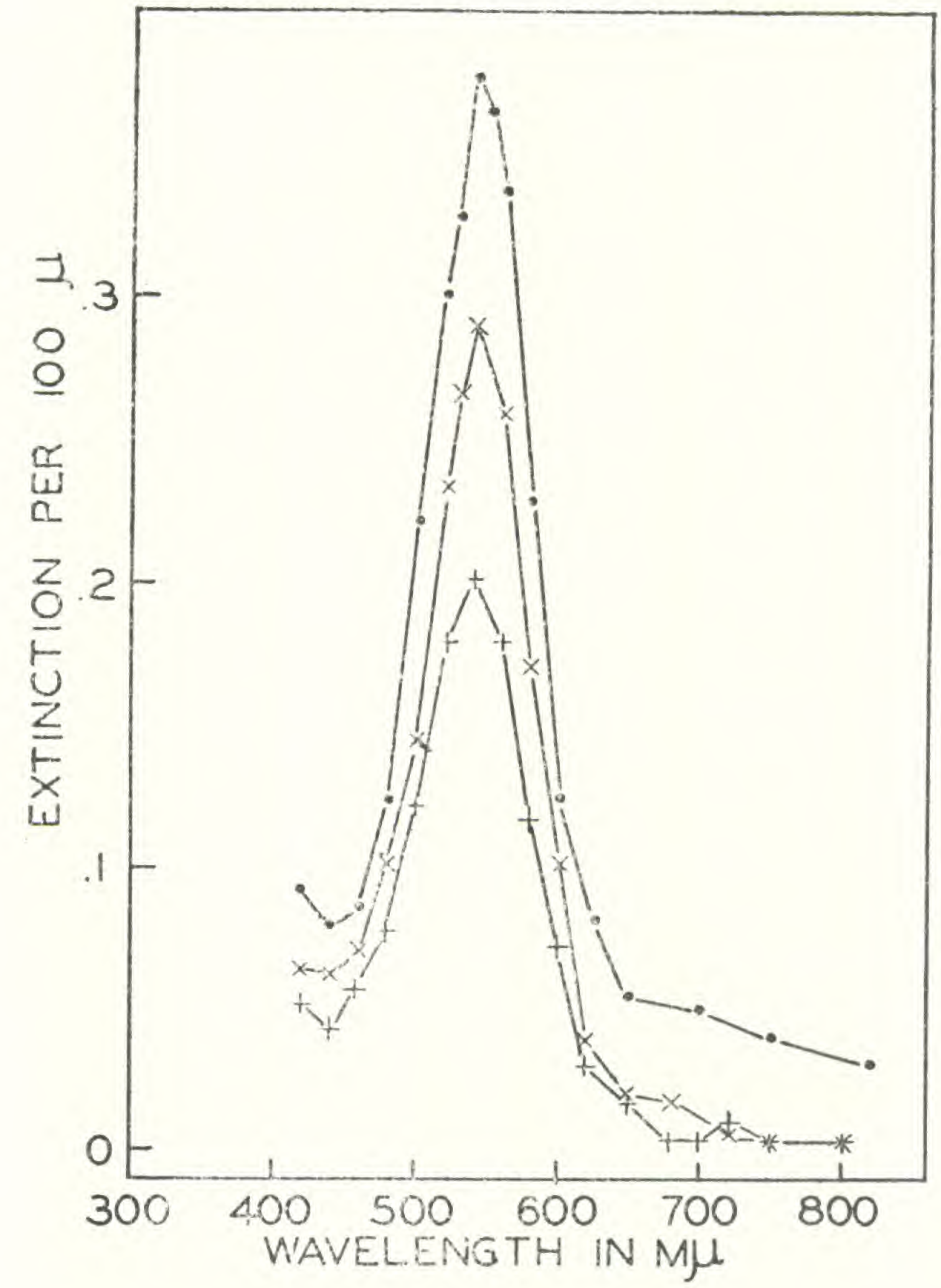

Fig. 3. Absorption spectra of three different epidermal cells from a *Coleus* leaf. The upper curve is for a flat epidermal cell, the center curve for the second cell of an epidermal hair, and the lower curve for the basal cell of the same hair.

calculation of cell volume. Finally, the varying diameter provides a ready means of testing the effect of thickness on optical density.

Epidermal hairs stripped from the midrib of mature leaves and mounted in distilled water under a thin cover glass were examined to locate cells not overlaid by any other tissue and oriented in a plane horizontal to the microscope's optical axis. By means of the ocular disc mounted in the side ocular, the cells' dimensions were determined. By reference to the same scale a point in the center of each cell was located. All measurements of optical density were made on these points. The absorption spectra of the selected cells were determined by the procedure outlined above.

Typical results of such measurements are shown in fig. 3. For the sake of uniformity the data are presented in terms of the optical density per 100 μ since the thickness of the cell at the point scanned will obviously alter the light transmission values. Figure 3 shows that reliable determinations of a characteristic band at 540 mμ can be obtained. According to Robinson (1931) the red color of the leaves of *Coleus Blumei* is due to an anthocyanin, cyanin. Purified preparations of cyanin have an absorption maximum at 510–520 mμ (see below), and it seemed likely therefore that this substance is responsible for the peak at 540 mμ exhibited by *Coleus* cells.

As a means of confirming this point, the effect of alkali on the cell absorption spectrum was studied. Cyanin in alkaline solution develops a deep blue color, and the absorption band is correspondingly shifted toward the longer wave-lengths. The absorption spectrum of a hair cell was determined in the usual way in the entire available spectral range of 340–800 mμ. The slide was then flooded with a dilute solution of ammonium hydroxide which caused the normal red color of the cells to give way to blue, and the absorption spectrum redetermined. The results, shown in fig. 4, indicate that the expected shift in the position of the visible absorption band does indeed occur. The addition of alkali shifts the peak from 540 mμ to 600 mμ.

Figure 4 also shows that in addition to the peak in visible light these cells have a second absorption maximum in the near-ultraviolet. In the normal cell this peak is at 360 mμ; in the alkali-treated cell it is broadened considerably with the maximum at about 380–390 mμ. It had been previously noted (by Mr. Milton Zucker of this laboratory) that *Coleus* hair-cells which are low in anthocyanin turn bright yellow on addition of alkali, suggesting that a flavone glucoside was present. All flavones have an absorption maximum in the region of 320–330 mμ, which in alkaline solution shifts to about 380 mμ. It seemed likely therefore that the cells' absorption maximum at 360 mμ represented flavone rather than anthocyanin.

To test this possibility, spectra were obtained from single hair cells of a green variety of *Coleus,* which shows no red color and appears to be free of anthocyanin. A series of spectra made on single hair cells from this type of plant revealed in each case an absorption maximum at 360 mμ. Typical results are shown in fig. 5. In

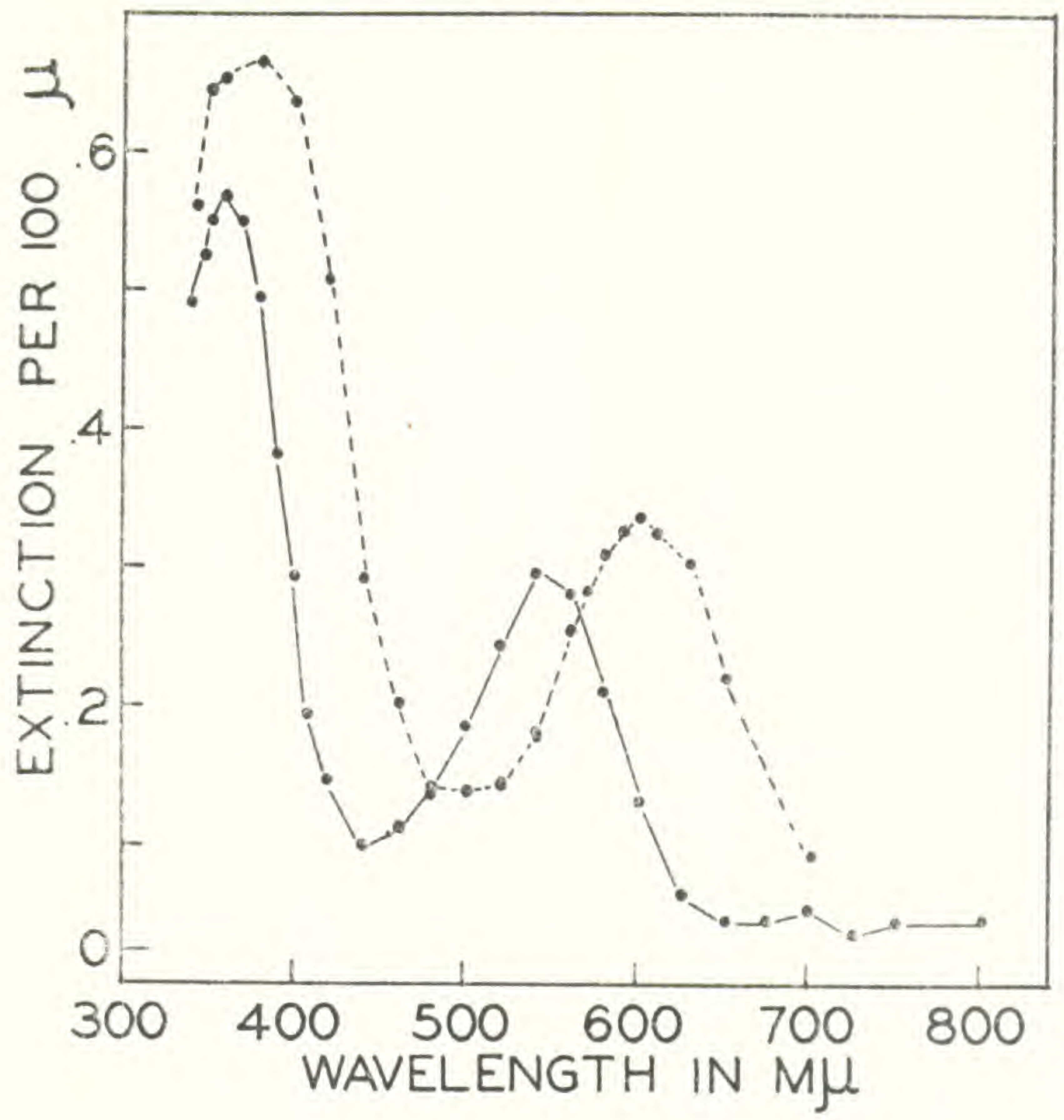

Fig. 4. The absorption spectrum for a hair cell (basal) from a red *Coleus* leaf in water (solid line) and ammonium hydroxide (dotted line).

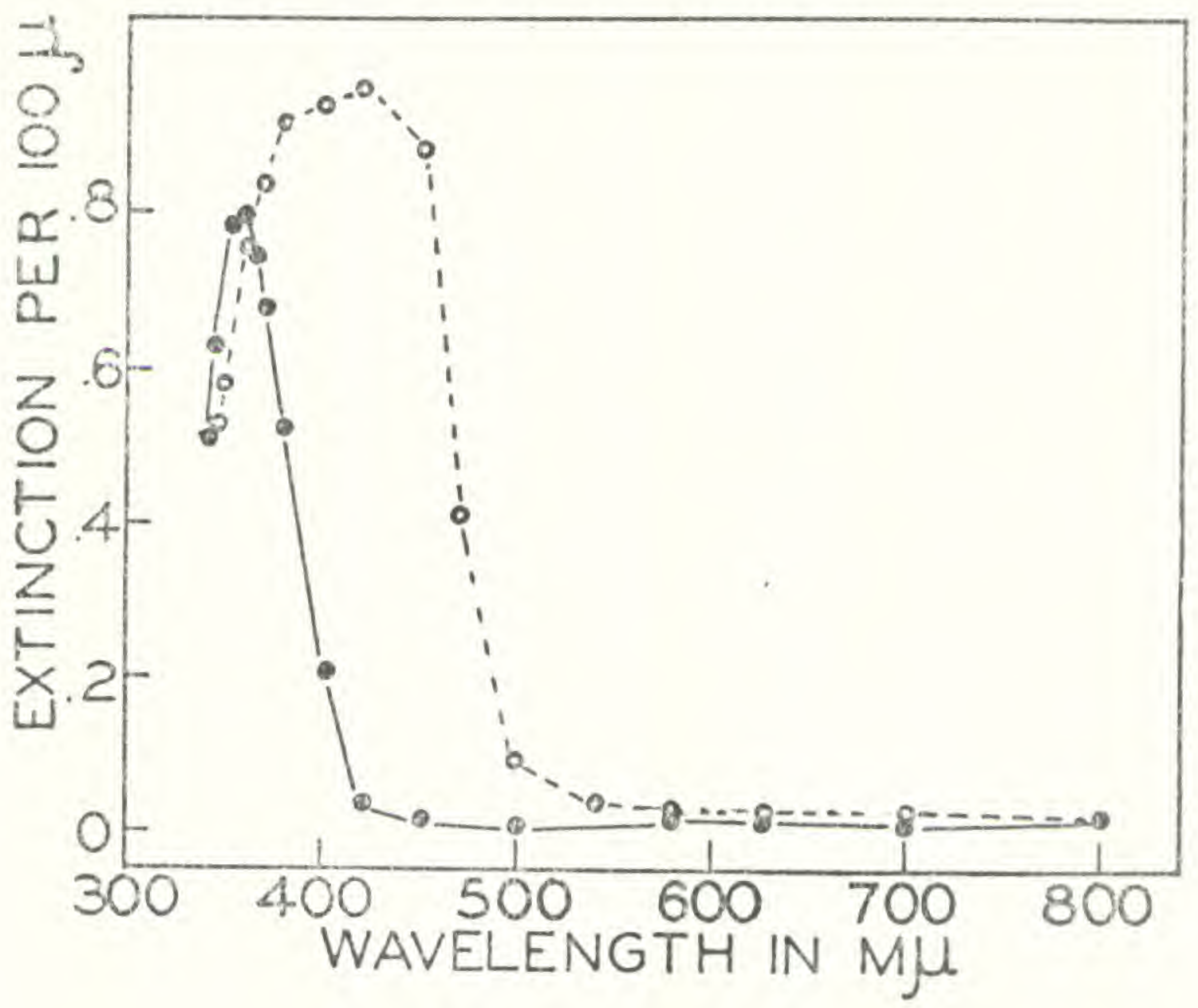

Fig. 5. The absorption spectrum of a hair cell (basal) from a green *Coleus* leaf in water (solid line) and ammonium hydroxide (broken line).

agreement with the gross observation that the green variety lacks anthocyanin, no obvious peak at 540 mμ is visible. (However, a small and possibly significant rise in optical density does occur at that wave-length, and this may indicate the presence of an extremely small amount of the anthocyanin which occurs in large quantities in the red varieties.) As also shown in fig. 5, the effect of ammonium hydroxide on the green *Coleus* hair cell was determined, and the shift of the maximum toward the longer wave-lengths is similar to that obtained in the red variety, though somewhat more marked.

From these data it seems clear that the absorption maximum of *Coleus* hair cells located at 360 mμ does not represent anthocyanin, but rather is due to a constituent common to the red and green varieties, probably a flavone. To obtain additional data on this point, the absorption spectra of extracts of both red and green varieties were determined (in a Beckman spectrophotometer). The extracts were prepared by boiling leaves in relatively large volumes of 1 per cent HCl.

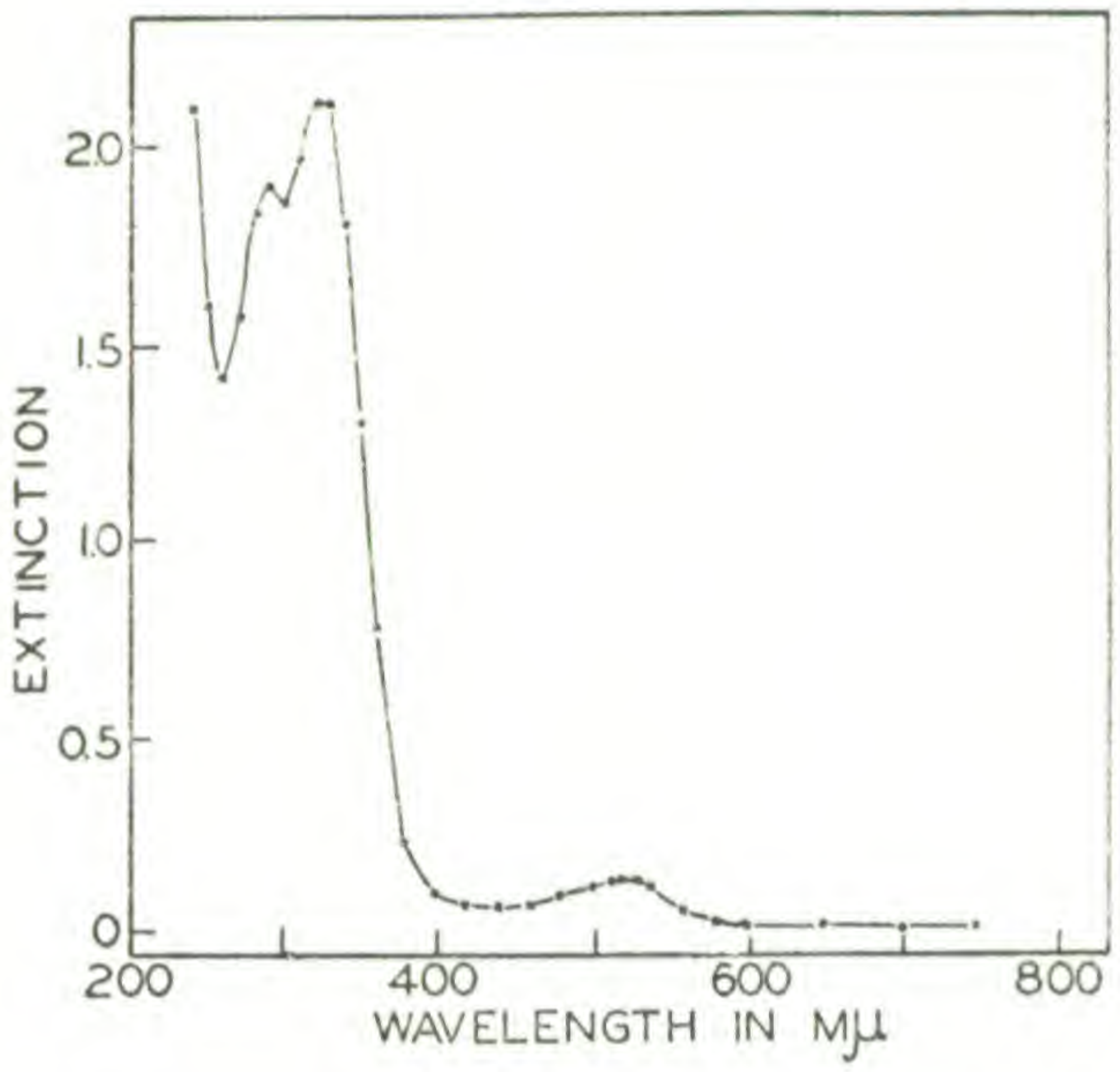

Fig. 6. Absorption spectrum of an extract of red *Coleus* leaves in 1 per cent HCl.

Figure 6 is the absorption spectrum of the extract of red *Coleus* leaves (in 1 per cent HCl). A band in the neighborhood of 520 mμ is obvious, but the absorption in the ultraviolet is considerably stronger, showing definite peaks at 290 and 325 mμ. Figure 7 (solid line) is the absorption spectrum of the extract of leaves from the green variety of *Coleus*. At pH 2 no absorption occurs in the visible range, but the two peaks at 290 mμ and 325–330 mμ in the ultraviolet are similar to those shown in fig. 6. Since the colorless extract of the green leaves lacks anthocyanin and yet exhibits the two ultraviolet maxima, it is again obvious that these maxima are not due to anthocyanin. That they may result from a flavone is again indicated by the second curve (dotted line) in fig. 7, which represents the absorption spectrum of the extract at an alkaline pH (8.4). The

maximum is shifted toward the longer wave lengths. Such alkaline solutions of the green *Coleus* extract show the yellow color characteristic of flavones at alkaline pH.

To separate the constituent pigments of the red *Coleus* extract the original solution was extracted with an equal volume of ethyl acetate (in which flavones but not anthocyanins are soluble). The ethyl acetate fraction was then shaken with phosphate buffer of pH 6.4 and the ultraviolet absorption spectrum of the aqueous layer determined. This is shown in fig. 8, and it is at once apparent that the constituent removed by the ethyl acetate does show the two peaks at 290 and 320 mμ. The buffer solution, upon being made alkaline, turns yellow and then brown, and so appears to contain a flavone.

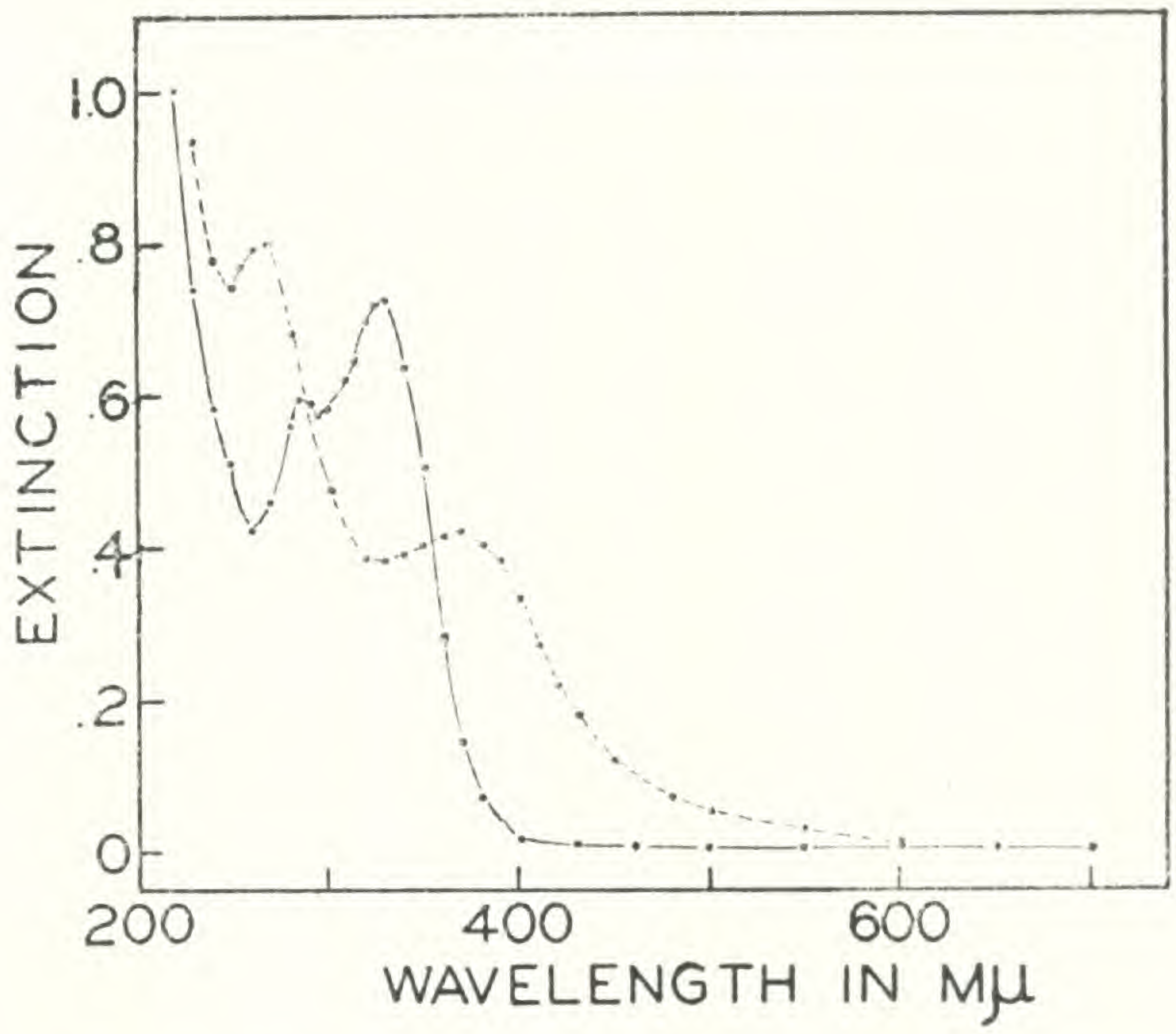

Fig. 7. Absorption spectrum of an extract of green *Coleus* leaves at pH 2 (solid line) and pH 8.4 (broken line).

These results suggest therefore that the red *Coleus* epidermal cells contain, in addition to anthocyanin, other material with absorption maxima (in acid solution) at 290 and 320–325 mμ, at least part of which is a flavone. This material is present in the cells of the green variety which lack anthocyanin.[1]

With this information at hand it is possible to reexamine the significance of the two absorption maxima obtained from intact living cells. In the first place, it will be noted that the anthocyanin maximum of the extract is at 520 mμ, while the maximum

[1] Further extraction experiments suggest that the peaks at 290 mμ and 320 mμ may be due to different substances. Repeated extractions of leaf preparations with ethyl acetate cause a progressive reduction in the 320 mμ peak of the original extract, but much of the 290 mμ absorption remains in the aqueous fraction. It is possible therefore that the 290 mμ peak is due to the ultraviolet absorption of anthocyanin (crystalline cyanin has a peak at 275–280 mμ). Furthermore, this peak may in part be due to the presence of a leucoanthocyanin, since recent reports (Fogel, 1948) suggest that these substances are characterized by absorption maxima at this wave-length.

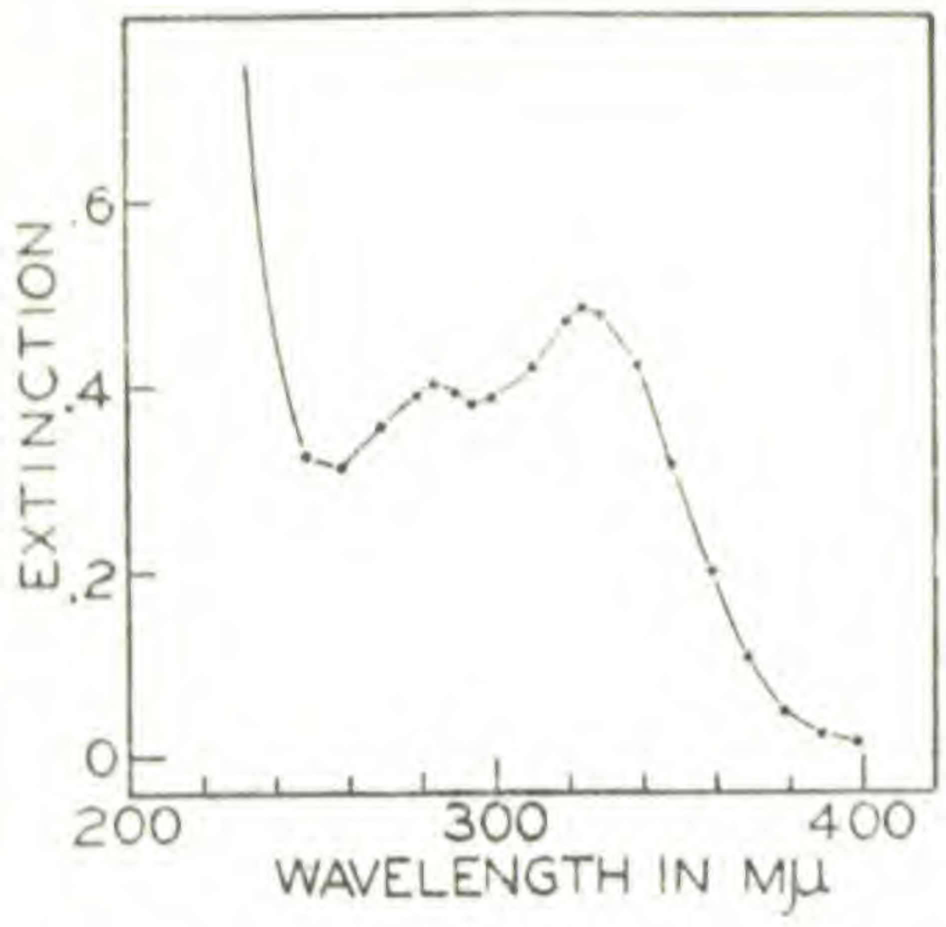

Fig. 8. Absorption spectrum of material removed from red *Coleus* extract by ethyl acetate. The sample was obtained by shaking the original extract with ethyl acetate and then extracting the ethyl acetate fraction with phosphate buffer of pH 6.4.

obtained in the living cell is at 540 mμ. This discrepancy has been confirmed repeatedly. The maximum of the extracted anthocyanin is not altered by purification procedures such as repeated extraction with ethyl acetate or lead acetate precipitation. Paper chromatograms of the extract yield only a single red-colored band, and this preparation also has a peak at 520 mμ. It seems reasonable to conclude therefore that the anthocyanin absorption represents a single substance which in solution (at acid pH) has a peak at 520 mμ. Since all of a considerable number of spectra of living cells yield a maximum at 540 mμ it is necessary to conclude that the *Coleus* anthocyanin within the cell is in some state other than the one found in solution. The acidity of the cell might seem to offer an explanation of this phenomenon. It can be seen from fig. 9 that the extract at pH 8.4 has a maximum at 590 mμ rather than 520 mμ, and it might be expected that the shift to 540 mμ shown by the cell may represent a pH effect. While this explanation cannot as yet be ruled out there is some evidence against it. Repeated attempts to shift the cell's peak to 520 mμ by flooding the cell with acetic acid have failed. Furthermore, even the peak at extremely alkaline pH is not the same in the cell (600 mμ) and extract (590 mμ). It seems possible therefore that the shift of

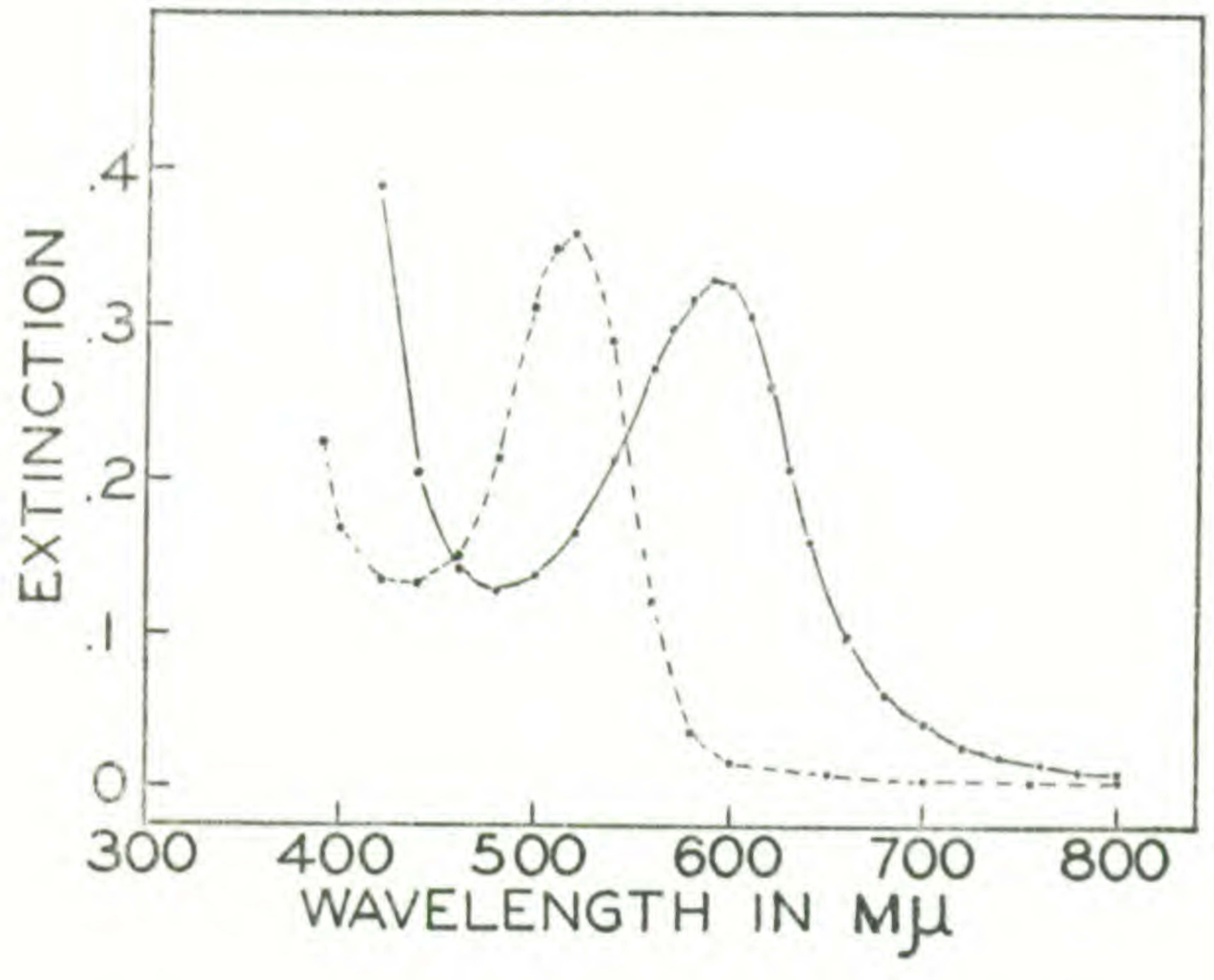

Fig. 9. The absorption spectrum of an extract of red *Coleus* leaves at pH 2 (broken line) and pH 8.4 (solid line).

absorption maximum characteristic of the cell may represent some effect other than that of pH. One possible explanation is that the anthocyanin in the cell is combined with some other cellular constituent, such as a protein, a phenomenon which frequently alters a pigment's molecular structure sufficiently to cause a significant shift in absorption maxima.

A similar discrepancy between the maxima of the extracts and the intact cell exists in the case of the non-anthocyanin absorption bands. The living cells have an absorption maximum at 360 mμ which shifts to 400–425 mμ in alkali; the extract's maximum at 320 mμ shifts to 370 mμ in alkali. In both cases the response to alkali is similar, suggesting that the substance responsible for the 320 mμ peak in the extracts accounts for the 360 mμ peak in the living cell. Again, this would suggest that the substance responsible for this absorption band—probably a flavone—occurs in the cell in some form of combination which does not exist in extract.

The possibility that the flavone and anthocyanin pigments in the living cell occur in a complex together with some other cellular constituent may have an important bearing on further analysis of the metabolic role of these substances.

From the evidence presented above it seems reasonable to conclude that the absorption maximum observed in living *Coleus* hair cells at 540 mμ which shifts to 600 mμ in an alkaline medium represents anthocyanin, and that the maximum found at 360 mμ which shifts to 420–425 mμ in alkali probably represents a flavone compound. It is therefore possible to use these facts as a means of making quantitative determinations of both anthocyanin and flavone content of single hair cells.

V. Determinations of Anthocyanin and Flavone Contents

The considerations necessary to effect accurate determinations of the concentrations of substances present in cells from measurements of the optical density are expressed by the Beer-Lambert laws of light absorption. These state that the amount of light energy absorbed is a function of the number of molecules (which specifically absorb light of the given wave-length) contained in the path of the light beam. Since each layer of the sample reduces the amount of light impinging on subsequent layers of the sample this relationship is logarithmic and is expressed by the equation:

$$E = \log_{10} 1/T = kcd$$

where E is the extinction or optical density; T is the fraction of incident light which emerges from the sample; c is the concentration of the specifically absorbing substance per unit volume of the sample; d is the thickness of the sample; k is a constant which expresses the tendency of the molecules of the specific substance to absorb impinging light energy of the given wave-length.

In the procedures described above, the optical measurement made is of T, while d is determined by measuring the thickness of the cell at the point scanned.

It follows from the above equation that the concentration of the substance present in the sample is proportional to the optical density per unit thickness, and that the ratio of the concentrations of two different samples is equal to the ratio of their respective E/d quotients. However, this relationship holds only when all of the light absorption is due to the presence of the specific substance in question. In ordinary spectrophotometric practice non-specific light losses are accounted for by comparing the sample with a "blank" which is identical with the sample except that it lacks the specific substance. This procedure cannot be followed in determinations of substances naturally occurring in a living cell and indirect methods must be used.

In general, two such methods can be applied: (1) The cell's non-specific light absorption may be determined at a wave-length outside the characteristic absorption band of the substance in question. It must then be assumed that this amount of non-specific light-loss also occurs at the wave-length of the substance's absorption maximum. This assumption may not be valid, particularly if the extrapolation is made into the ultraviolet range. In the case of the present measurements, however, it would seem relatively safe to assume, for example, that the non-specific light loss at the anthocyanin maximum (540 mμ) is equal to the light absorption in red light where the cell (since it is free of chlorophyll) contains little specifically absorbing material. The validity of applying this assumption to the absorption at 360 mμ is more doubtful.

(2) A second method is the conversion of the substance in question into a new molecular form in which it exhibits an absorption maximum at a new wave-length. Thus, addition of alkali shifts the flavone absorption band in the cell from 360 mμ to about 400–420 mμ. Hence the cell's optical density at 420 mμ can be measured at a normal pH and again after addition of ammonia. The difference between the two values of E is then an accurate measure of the relative flavone concentration of the cell. This method can also be applied to the determination of anthocyanin by measuring the cell's extinction value at 625 mμ before and after addition of alkali. The data presented below are intended to examine the relative validity of both methods as a means of determining anthocyanin and flavone concentrations in single cells.

In the first instance it is necessary to determine whether the total optical density of the cell is indeed a linear function of the thickness of the area scanned. This problem was examined by making use of the conical shape of the *Coleus* hair cells. Assuming that the anthocyanin concentration is uniform throughout the entire volume of the cell, it is possible to study the effect of cell thickness by taking absorption readings at various points along the length of a single cell, thereby obtaining a graded series of thicknesses through a sample of identical pigment concentration. If the test object follows the Beer-Lambert laws, the plot of extinction versus thickness should follow a straight line. Several

typical sets of such measurements are shown in fig. 10, and it is clear that the data do conform to the expected optical relationship.

To test the relative validity of the methods outlined above, the following determinations were made on nine *Coleus* (red) hair cells selected at random from strips of midrib epidermis.

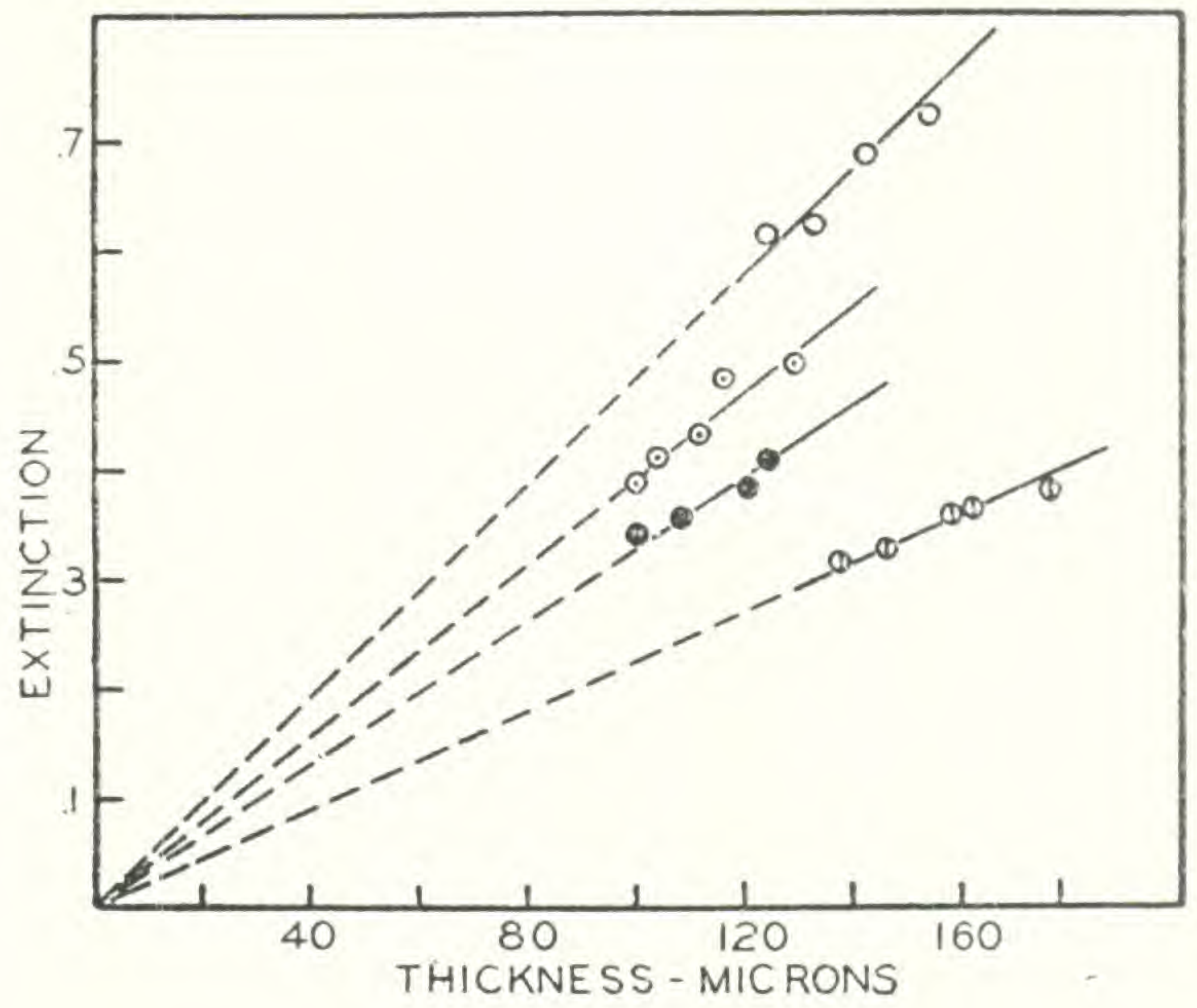

Fig. 10. The extinction (at 540 mμ) of each of four different red *Coleus* hair cells at various thicknesses. Since the cells are conical in shape, areas of different thicknesses could be scanned by focusing on various points along the cells' long axes.

With the cells mounted in water, the value of E per 100 μ of cell thickness was determined at wave-lengths 700 mμ, 625 mμ, 540 mμ, 440 mμ, 420 mμ, and 360 mμ. The slide was then flooded with ammonium hydroxide and the E per 100μ values for the same cells determined at 625 mμ and 420 mμ.

From these data the relative anthocyanin concentration of each cell was calculated by the two methods:

(1) Relative anthocyanin concentration $= E_{540} - E_{700}$.

(2) Relative anthocyanin concentration $= E_{625}$ (ammonia) $- E_{625}$.

The relative flavone concentrations were also calculated by the alternative methods:

(1) Relative flavone concentration $= E_{360} - E_{440}$.

(2) Relative flavone concentration $= E_{420}$ (ammonia) $- E_{420}$.

The two sets of values obtained for the relative anthocyanin concentration of the cells are plotted against each other in fig. 11. It is quite clear that both procedures give the same value for the anthocyanin content and it seems valid to use the extinction value at 700 mμ as a measure of the non-specific absorption at 540 mμ.

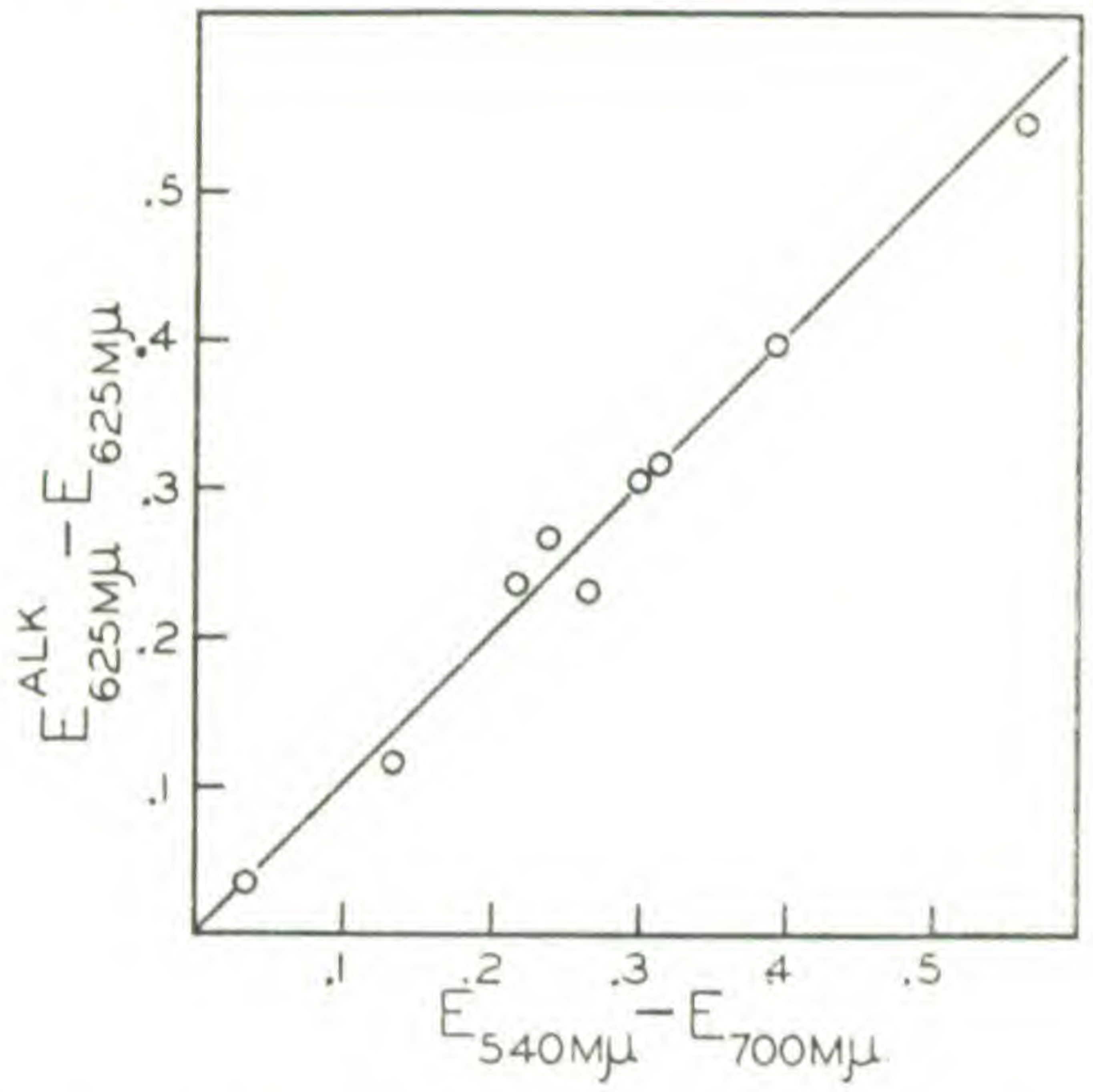

Fig. 11. The relationship between values obtained for the relative anthocyanin concentrations of nine hair cells by two different procedures. The abscissa represents relative anthocyanin concentrations determined from the difference between the cells' extinction values (in water médium) at 700 mμ and 540 mμ. The ordinate represents the corresponding values obtained by determining the difference between the same cells' extinction at 625 mμ in ammonium hydroxide and their extinction at 625 mμ before being treated with alkali.

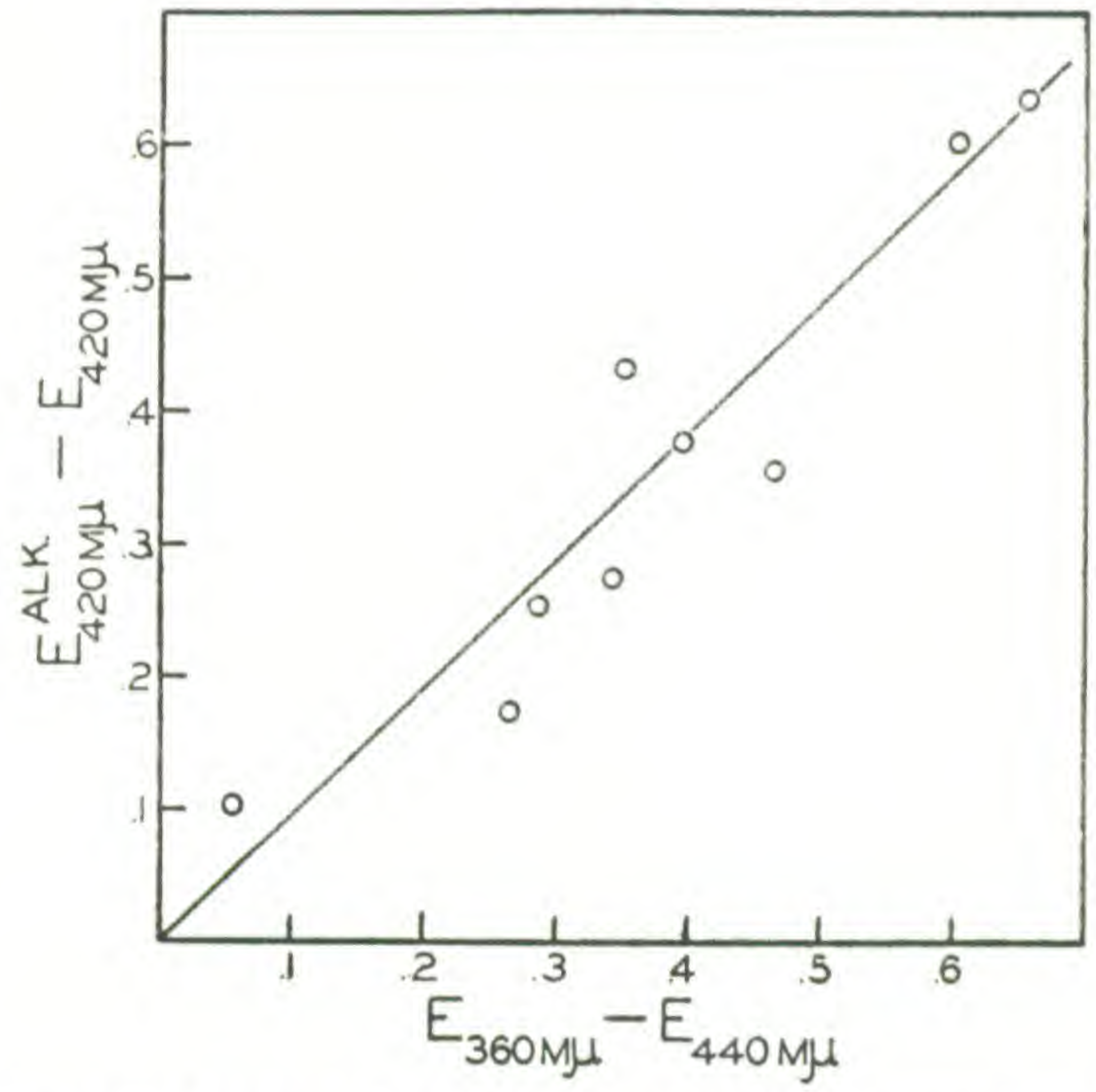

Fig. 12. The relationship between the flavone concentration of nine *Coleus* hair cells determined by two different procedures. The abscissa represents the relative flavone concentrations determined from the difference of the cells' extinction (in water medium) at 360 mμ and 440 mμ. The ordinate represents the corresponding values determined from the difference between the same cells' extinction at 420 mμ in ammonium hydroxide and their extinction at 420 mμ before being treated with alkali.

A similar plot of the flavone data is shown in fig. 12. These points show a significant amount of scatter from the line of proportionality, a result expected from the fact that the measurements were made in the near ultraviolet. Apparently there is a significant amount of random non-specific light loss at this wavelength, and the reliability of the 440 mμ extinctions as a measure of non-specific absorption at 420 mμ is lower than that for the corresponding treatment of the anthocyanin data. Hence while determinations of anthocyanin content may be made without recourse to alkaline treatment, the use of a pH shift seems necessary for flavone estimations.

VI. Discussion

The evidence presented above shows that it is possible, by use of rapid spectrophotometric measurements, to identify and determine the concentration of anthocyanin and flavone in single cells. These results can undoubtedly be applied to determinations of other substances as well. Preliminary experiments show that chloroplast pigments may be identified and estimated by the same procedure.

Furthermore, the method is applicable to determinations of metabolic rates in single cells. Thus the rate of decolorization of methylene blue can be followed in a single cell, and the activity of cellular dehydrogenases thereby determined. Preliminary measurements of this kind made on epidermal cells show that accurate determinations of rates of dehydrogenation can be made within an hour. Corresponding measurements have been made with tetrazolium chloride, a substance which forms a red formazan as a result of dehydrogenase activity.

Such quantitative determinations of various metabolically important substances and rates of reactions in single cells can yield valuable data on questions of cellular differentiation and physiological genetics, and should be applicable to other types of investigation as well.

VII. Summary

(1) A microspectrophotometer of relatively simple construction is described.

(2) The instrument is capable of determining absorption spectra of 4 μ areas of single cells over the spectral range of 340–800 mμ. Its accuracy relative to macro determinations with a Beckman spectrophotometer is demonstrated.

(3) The presence of anthocyanin and flavone in single hair cells of *Coleus* has been demonstrated by such absorption spectra. The absorption maxima of these substances in the living cell is different from those of the substances in solution. It is suggested that this discrepancy may indicate that these substances are combined with some other cellular constituent *in vivo*.

(4) Methods for quantitative determination of anthocyanin and flavone in single cells are presented. Anthocyanin concentrations may be determined in living untreated cells. Flavone estimations are more accurate if determined from the effect of alkali on the substance's absorption maximum.

(5) The microspectrophotometer offers many possibilities of measuring significant metabolic rates in single cells.

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THE SOUTHERN DENT CORNS

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The older maize varieties of the southern United States are of interest for two reasons: (1) Some of them were extensively used in developing the more highly derived varieties of the United States corn belt. (2) They show a strong affinity to the dent corns of central Mexico. When their history can be worked out in more detail, it should shed significant light on the relationships of the brilliant civilizations of central Mexico and the lands to the north.

In the states east of the Mississippi, maize has had, on the whole, a relatively simple history. As we have demonstrated (Brown & Anderson, 1947), the northern flints were widely distributed in pre-Columbian times in the northeastern states where they were the only type of corn grown over a considerable area. In the Gulf States and spreading northward from them, there were at least two other major types of maize: (1) the old white dents, and (2) the Caribbean flints. We do not yet have any exact knowledge of when the intermingling of these southern types began. We do know that by the early nineteenth century the old southern dents were, on the one hand, being intentionally crossed with the Caribbean flints and, on the other hand, with the northern flints. From the latter union there was eventually developed the distinctive, cylindrical dent corn of the United States corn belt.

Today in the southern states one may still find authentic samples of such old dent varieties as Gourdseed and Shoepeg. They are not easy to come by and require extensive searching among conservative families in more or less isolated neighborhoods. Along with them are more modern varieties derived from crosses with the northern flints, with Caribbean flints, and with corn-belt varieties from farther north. For the purpose of this study we have made a rough grouping of the material under observation as: (1) old southern dents, (2) derived southern dents. Our collections of these corns were reasonably complete and our survey is a comprehensive one, particularly in relation to the role played by these varieties in the development of the maize of the United States corn belt. The Caribbean flints, although undoubtedly involved, were peripheral to the area covered by our studies and have therefore been omitted from this survey. These tropical flints, because of their wide distribution in both hemispheres, deserve exhaustive analysis, but to be carried on effectively such a study would require adequate experimental fields in a subtropical environment.

The methods used in this study were essentially those applied to previous surveys of maize in the United States and Latin America. A few selections were

grown and observed over a period of years. In the winter of 1946-47 an intensive effort was made to get together as representative a collection as possible, including large field samples, to show the range of variation. The collection was grown in duplicate at Gray Summit, Missouri, and at Johnston, Iowa. For each culture, photographs were made of representative plants, of representative tassels, ears, and kernels. The variation of the tassel was observed and recorded in detail, and the chromosome knob number was determined from pachytene smears. Much of this information is presented below in tabular summaries.

History

Compared to the northern flints, the history and archaeology of the southern dents are in a very unsatisfactory state. There are several clear descriptions of the northern flints in the pre-colonial and colonial literature, and over a wide area in the eastern states they are the only archaeological type which has yet been discovered. The dents are a variable lot. We would need to have many more archaeological specimens if we were to do equally as good a job with them as with the northern flints, and as yet we have almost none. From those specimens which we have been able to examine, it is certain that dented varieties were grown in the Great Plains in pre-historic and proto-historic times. The story of corn in that area is apparently a very complicated one. Not until the archaeology of that region is better understood and not until we have seen many more collections which include maize remains will we be in a position to discuss the early history of dent corns in the region now occupied by the United States. For the states east of the Mississippi where we have descriptions of strongly dented varieties in early colonial times, we have as yet seen no archaeological material. As far south as Alabama and Georgia the archaeological record (away from the Mississippi Valley) is made up of wide-seeded flint or flour corns of the same general type as the "northern flints" of New England and Canada. This suggests that the dented varieties described in the Colonial records were relative newcomers and were in the process of pushing northward and eastward at the time of European contact.

Apparently the earliest description of a southern dent corn is in Beverly's history of Virginia written in 1705. He wrote that it is: "a larger grain and looks shriveled with a dent on the back of the grain as if it had never come to perfection; and this they call She corn." In the agricultural note books of Charles Read of New Jersey occurs the earliest reference we have been able to find to dent corn described as such. In an entry for 1756 he lists the weights of various kinds of corn, among others, "Egg-Harbor Dented" and "the long-grained, Lower County corn." (See Woodward, 1941).

At about this same period we have a fairly good description of a deeply dented white corn from Louisiana. Dumont, in his *Mémoires historiques sur la Louisiane*, published in 1753, has the following description (pp. 32–34):

"On distingue deux sortes de mahi, dont l'un est propre à faire de la farine, & l'autre non: ce dernier a le grain tout rond; l'autre l'a un peu plus plat, & se distingue par une espéce de coup d'ongle ou de rainure qui regne sur toute la longeur des graines." [Two kinds of maize can be distinguished, one good to make meal, the other not. The latter has the kernel quite round, the other is a little more flat and is distinguished by a kind of claw point or groove prevailing along the whole length of the kernel.]

John Lorain, whose shrewd observations on maize and maize breeding were unsurpassed until long after his time, provides us with the first detailed description of gourdseed varieties. In a letter dated October 25, 1813, and published in the *Memoirs of the Philadelphia Society for Promoting Agriculture* (Vol. III, pp. 308–310) he described Gourdseed:

"The cob of this is neither so long or thick as the large solid corns but the grains are very long, forming a compact, round and gradual taper to a point where they join the cob. It is vastly more productive than any other known original corn but ripens late and the grains are too soft and open for exportation, unless kiln dried. This variety, so far as my observation goes, is invariably white; for although I have frequently heard of a solid yellow gourdseed corn, yet on investigation, nothing more has appeared than a mixture of the hard yellow corns with the white gourd seed."

In his book on agriculture published posthumously in 1825 Lorain goes into greater detail. He describes the gourdseed varieties as having up to 32 and sometimes even 36 rows of kernels. The results to be obtained from mixing gourdseeds and northern flints were accurately described in considerable detail and the benefits of such a mixture were clearly set forth.

Lorain's writings clearly indicate that the purposeful (as well as accidental) mixing of gourdseeds and flints was already well under way in the early 1800's. From the agricultural press and such early scientific agencies as the U. S. Patent Office and the State Agricultural Reports, one can reconstruct quite accurately the history of the dent varieties of the United States corn belt. Some of the main evidence has already been reviewed in our survey of the northern flint corns and need not be repeated here. We can summarize the results, in so far as the United States corn belt is concerned, by saying that the northern flints and southern dents (originally two very different types of maize) were so repeatedly crossed and recrossed that the mixtures bred from them eventually dominated the entire region. Today the 8-rowed flints are grown, if at all, only in the extreme north, and the gourdseeds and shoepegs have completely disappeared from the actual corn belt. Their very names have been largely forgotten, and even in the southern states it is only a few conservative families who still grow them.

Cytology

A cytological peculiarity of maize is that at certain points on the chromosomes there may be definite knobs of more deeply staining material. The knob number is constant for any individual plant and in the corn of the United States may vary from 0 to about 14 (haploid number). It can therefore be used as one criterion in determining the relationships of various kinds of maize.

The number of chromosome knobs was determined for each of the varieties included in this study. Knob counts were, without exception, made from temporary smears of pachytene chromosomes stained either with aceto-carmine or propionic-carmine. Since the seed from which our cultures were grown was from open-pollinated stocks, they exhibited considerable morphological and cytological variability, as might be expected. For purely physical reasons, where several cultures are involved, it is impracticable to determine knob numbers of a large number of plants of each culture. The data on knob numbers reported herein were taken from two to four plants of each variety and show primarily the overall range of variability between varieties. Had we worked with larger numbers of plants we possibly would have encountered a greater degree of variation within some varieties than is reported.

As is often true, some difficulty was encountered in distinguishing between large chromomeres and small knobs. Our policy has been to count as knobs only those pycnotic enlargements that are strikingly larger than the average chromomere. This practice has been followed even when the enlargement was located at a known knob position. For this reason our counts should be taken as conservative. Since the organizer knob on chromosome No. 6 is present in all strains of maize, we have excluded it in our enumerations of knob number.

It will be noted that knob numbers in this material range from 4 to 12. When the varieties are separated into (1) old southern dents, and (2) derived southern dents, it is immediately apparent that the majority of the high knob varieties are to be found among the first group while those with lower numbers are mostly distributed among the derived southern dents (fig. 1). This association is to be

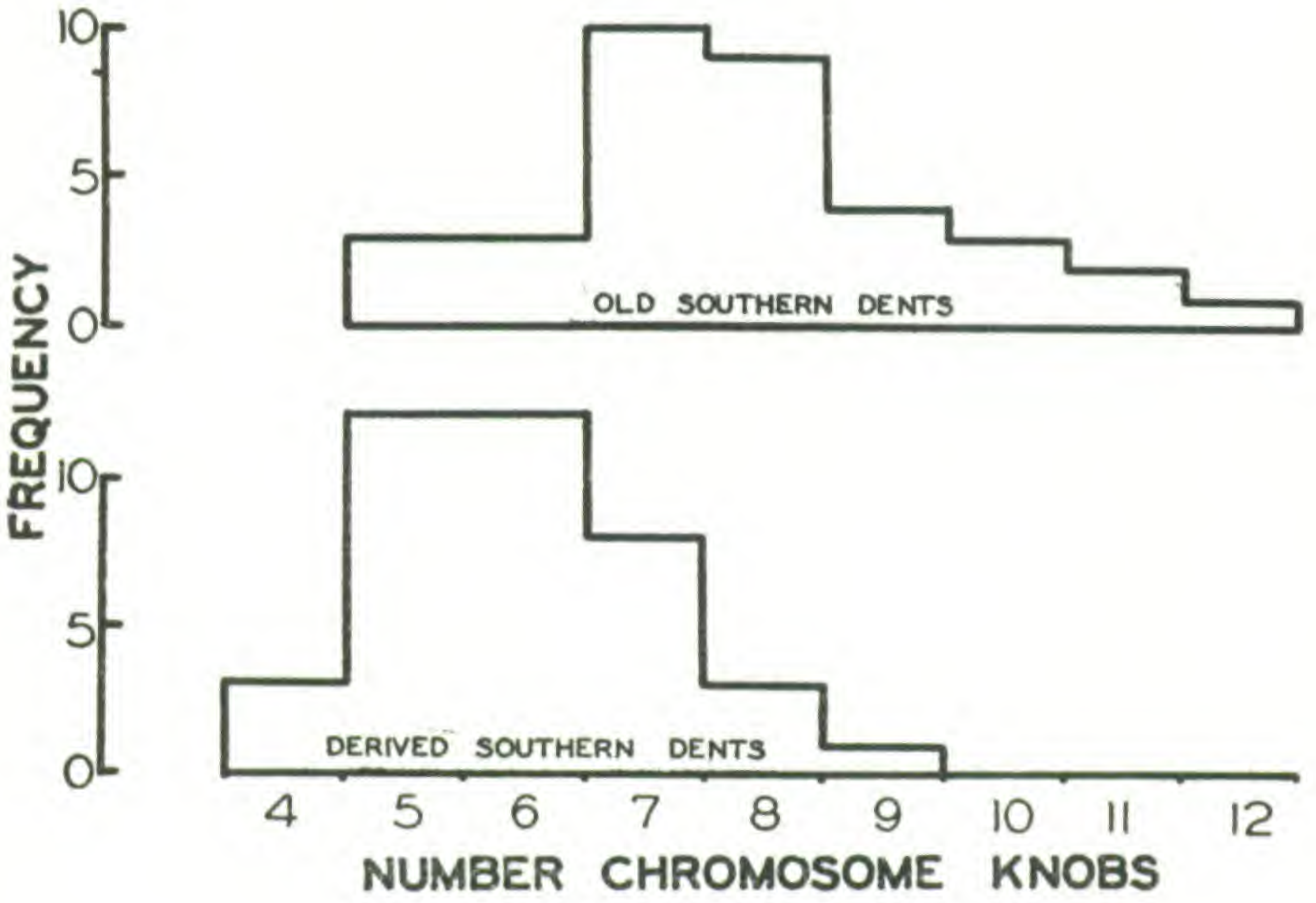

Fig. 1. Distribution of chromosome knobs in southern dent corns.

expected when we take into consideration the history of these two groups of corns. The old southern dents have evolved without drastic change from varieties of central Mexico which are known to possess relatively high numbers of chromosome knobs, while those types we have termed derived southern dents have largely arisen, either at first or second hand, out of crosses between old southern dents and northern varieties with lower knob numbers.

Morphology

The southern dents differ from the northern flints and from corn-belt dent varieties by a number of gross morphological characters, of which the following are more obvious. Plants of most southern varieties are unusually tall as compared to other United States corns. This is true whether we study them in the south or grow them farther to the north. The increased height is due to the presence of more nodes and not to an increase in internode length. In fact, most southern dents resemble Mexican dents in having extremely short internodes above the ear as compared to the long upper internodes of the northern flints (figs. 2–3). Ears are carried high on the culms and are enveloped in tight, thick husks which often extend well beyond the ends of the ears. Husks are usually composed solely of modified leaf sheaths, the blade portion of the husk being only slightly developed, if at all, and as a result one never finds the extensive "flag leaves" that are so common in northern flints. As a group the southern dents do not have tillers, although there are strains, particularly among the derived sorts, that occasionally produce a few. Prop-roots are well developed, and in certain of the more Mexican-like varieties they may be found even at the sixth and seventh nodes when they are grown in the north.

In contrast to the northern flints and most corn-belt maize, the tassels of the southern dents are many-branched and often highly condensed[1] (pls. 20–21). In many varieties the secondary branches are upright and comparatively short, resulting in a "whisk broom" appearance that is rarely found in the northern flints. In general, the numbers of tertiary branches in the tassels of southern dents are much greater than in the northern flints or corn-belt dents.

Most southern dents have a white endosperm although one or two varieties in our collection had yellow. According to the best historical evidence, the older southern dents were all white and the occurrence of yellow endosperm in the more modern strains is the result of outcrossing to yellow varieties. Although cob color is predominantly white, a few exceptional varieties with red cobs were represented in our cultures.

As mentioned above, we have rather arbitrarily divided our collection into (1) old southern dents, and (2) derived southern dents. In the second group we

[1]We are here referring to "condensation" in the technical sense, as defined by Anderson (1944); a condensation (or telescoping) of successive internodes on the tassel branches.

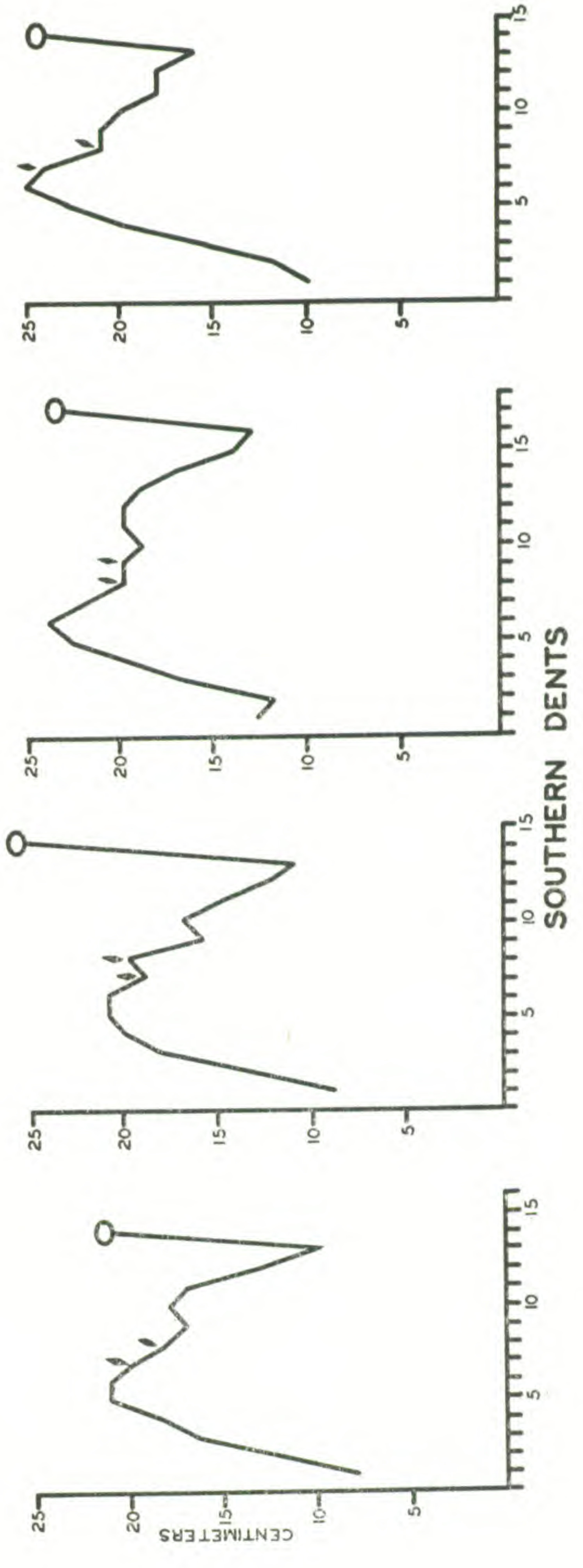

Fig. 2. Internode diagrams of typical individuals of four varieties of southern dent corns. Note the presence of many short internodes above the ears as contrasted to the long upper internodes of the northern flints (fig. 3).

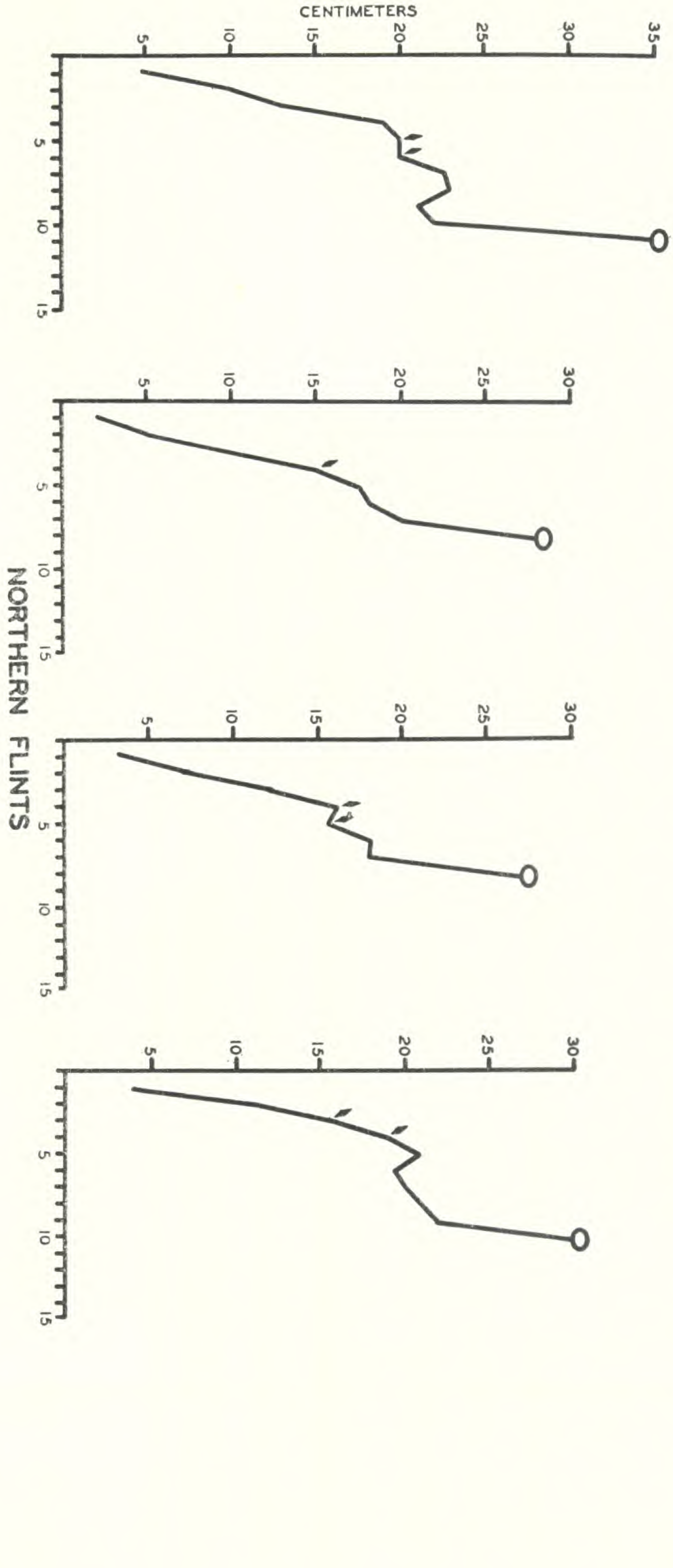

Fig. 3. Internode diagrams of typical individuals of four varieties of northern flint corns.

have placed those varieties whose morphology or whose known history indicates that they were derived by mixing southern dents with Creole flints, northern flints, or varieties from the corn belt.

Old Southern Dents.—

The old southern dents themselves do not form a homogeneous group. Three main types are represented, each one apparently derived from similar varieties which were and are grown in Mexico.

A. *Gourdseed and Shoepeg.*—These names are applied to rough white dents, which, on the whole, are much alike and may represent two extremes of the pointed-kerneled dent corns which are widely known in Mexico as "*pepitillo.*" Both of them are so strongly dented as to be collapsed at the pointed tip of the kernel. The gourdseed's kernel, though long and pointed, is also flattened with somewhat rounded sides, so that it looks not unlike the white seed of a cucurbit, hence its popular name. The shoepegs are the opposite extreme. The seed is very

TABLE I
VARIETIES OF OLD SOUTHERN DENTS

Variety	Source	Cob Color	Pericarp	Aleurone	Endosperm	Kernel width (mm.)	K. width/ K. th. (mm.)	Denting*	Mean row number	Number chromosome knobs
Gourdseed	Texas	White	Colorless	Colorless	White	7.1	2.3	5	18.1	6,7,8
Hickory King	Va.	White	Colorless	Colorless	White	13.0	3.4	3	8.4	7
Hickory King	Ga.	White	Colorless	Colorless	White	12.3	3.4	2	8.0	6,11,12
Hickory King	Tenn.	White	Colorless	Colorless	White	12.5	3.5	3	8.0	5,7,8
Jellicorse	Va.	White	Colorless	Colorless	White	7.6	2.1	4	12.7	9
June Corn	La.	White	Colorless	Colorless	White	7.0	2.1	2	14.2	10,11
Mexican June	Tenn.	White	Colorless	Colorless	White	8.0	2.2	2	13.8	7,8
Mexican June	Tenn.	White	Colorless	Purple & colorless	White	7.7	2.2	2	14.6	9
Old White Dent (1)	Ark.	White	Colorless	Colorless	White	7.8	2.2	4	16.0	5
Old White Dent (2)	Ark.	White	Colorless	Colorless	White	8.2	2.5	3	15.5	5
Red Cob Chisholm	Texas	Red	Colorless	Colorless	White	9.0	1.8	3	14.3	10
Shoepeg	La.	Red	Colorless	Colorless	White	5.0	1.5	5	18.3	7,8
Shoepeg	La.	Red	Colorless	Colorless	White	6.2	1.7	5	20.0	6
Shoepeg	La.	Red	Colorless	Colorless	White	5.2	1.6	5	18.6	7
Tenn. Red Cob	Tenn.	Red	Colorless	Colorless	White	7.1	2.2	4	14.4	7,8
Tuxpan	La.	White	Colorless	Colorless	White	7.2	2.1	3	14.8	7,8,9
Tuxpan	Va.	White	Colorless	Colorless	White	7.0	2.2	3	14.2	8
White Dent	Ark.	Red	Colorless	Colorless	White	7.0	2.6	4	16.0	7
Yellow Shoepeg	La.	Red	Colorless	Colorless	Yellow	5.2	1.6	5	19.6	7,8,9,10
Yellow Tuxpan	La.	White	Colorless	Colorless	Yellow	8.0	2.1	2	14.0	8

* 0—No soft starch at apex of kernel.
1—Soft starch but no denting.
2—Soft starch and a small dent.
3—Soft starch and a deep dent but no wrinkling of pericarp.
4—Soft starch and wrinkling pericarp.
5—Soft starch and the apex of kernel collapsed.

long and narrow, the sides being almost parallel, and it is pointed at the tip, the point itself usually being turned toward the apex of the ear by the tight husks to form a distinct hook at the top of the kernel (pl. 21).

The gourdseeds and shoepegs may well have been selected from the same fundamental stock and probably represent extremes of the same gourdseed type. The names, however, have been used to distinguish them for many years. The measurements (Table I) and accompanying photographs (pls. 20, 21) are drawn from samples collected in Louisiana and Texas.

TABLE II
VARIETIES OF DERIVED SOUTHERN DENTS

Variety	Source	Cob Color	Pericarp	Aleurone	Endosperm	Kernel width (mm.)	K. width/ K. th. (mm.)	Denting*	Mean row number	Number chromosome knobs
Cambren	Ky.	White	Colorless	Colorless	White	8.0	2.1	3	10.0	6
Caraway's Prolific	La.	Red	Colorless	Colorless	Yellow	6.5	1.9	3	14.3	6,7
Cherokee	Ga.	White	Colorless	Colorless	White	6.7	2.1	3	15.3	5
Clark's Yel. Dent	Texas	Red	Colorless	Colorless	Yellow	8.4	2.5	4	14.4	5,6
Columbia Beauty	Tenn.	Red	Colorless	Colorless	White	6.9	2.2	4	16.8	6
Garretts 1	Ky.	Red	Colorless	Colorless	White	7.0	2.1	3	15.1	5,6
Garretts 2	Ky.	Red	Colorless	Colorless	White	7.2	2.2	3	15.3	7
Giant Yel. Dent	Texas	Red	Colorless	Colorless	Yellow	9.7	2.7	4	12.5	5
Huffman	Tenn.	White	Colorless	Colorless	White	7.5	2.0	3	16.0	5
Jarvis Gol. Prolific	Tenn.	White	Colorless	Colorless	Yellow	7.2	2.0	2	14.0	5
Jarvis Gol. Prolific	Miss.	White	Colorless	Colorless	Yellow	7.3	2.1	2	12.7	4
Johnston Co. White	Mo.	White	Colorless	Colorless	White	7.7	2.0	5	18.0	7
Latham's Double	Va.	Red	Colorless	Colorless	White	5.8	1.8	3	14.8	6
Mammoth Ensilage	Va.	White	Colorless	Colorless	White	8.0	2.3	4	14.5	5
Mosby's Prolific	Va.	White	Colorless	Colorless	White	6.8	2.1	4	16.1	7,8
Mosby's Prolific	Miss.	White	Colorless	Colorless	White	7.0	2.2	2	13.5	5
Mosby's Prolific	La.	White	Colorless	Colorless	White	6.7	2.0	3	12.2	7
Mosby's Prolific	Tenn.	White	Colorless	Colorless	White	6.9	2.1	3	13.7	6
Neal's Paymaster	Ark.	White	Colorless	Colorless	White	6.8	2.1	4	15.6	6
Neal's Paymaster	Miss.	Red	Colorless	Colorless	White	7.4	2.2	4	14.7	6
Sherman	Tenn.	White	Colorless	Colorless	White	6.5	2.1	3	14.8	5
Southern Ill. 1	Ill.	White	Colorless	Colorless	White	9.0	2.6	3	13.6	5
Southern Ill. 2	Ill.	Red& White	Colorless	Colorless	White	7.0	1.5	3	15.3	6,7
Southern S'flake	Va.	White	Colorless	Colorless	White	6.6	2.2	3	17.0	5
Southern Yel. Dent	Miss.	Red	Light yel.	Colorless	Yellow	7.1	2.1	3	16.0	4,5
Strawberry	Texas	Red& White	Var'gated	Colorless	Yellow	7.9	2.4	3	14.6	8,9
Va. Horsetooth	Va.	White	Colorless	Colorless	White	6.2	1.8	3	17.7	4,6,7
Whatley's Prolific	Va.	Red	Colorless	Colorless	White	7.4	1.7	3	15.1	7,8
Yellow Dent	La.	White	Colorless	Colorless	Yellow	8.1	2.5	3	11.1	6
10 Row Dent	Ark.	Red	Colorless	Colorless	White	7.8	2.2	3	13.2	5

* 0. No soft starch at apex of kernel.
1. Soft starch but no denting.
2. Soft starch and a small dent.
3. Soft starch and a deep dent but no wrinkling of pericarp.
4. Soft starch and wrinkling pericarp.
5. Soft starch and the apex of kernel collapsed.

B. *Mexican June Complex.*—This category includes a rather closely related group of corns, the better known of which bear such varietial names as Mexican June, June Corn, Jellicorse, and Tuxpan. Although considerable variation exists within and between varieties, the group may be characterized and distinguished from the gourdseeds and shoepegs by having fewer rows of kernels and a lower degree of denting. Row numbers are usually 12 to 14. Ear shape varies from almost cylindrical to a very strong taper. The base of the ear is frequently compressed, and there is a tendency for slight irregularity in rowing at the base. The kernels are usually longer than wide and are slightly pointed. There is always a distinct cap of soft starch at the tip of the seed, bearing a small to medium dimple dent. Cobs are usually white.

This group of varieties is as Mexican-like as any in our collection. In ear type they are very similar to collections from central Mexico that have been classified by Anderson (1946) as intermediates between Mexican Pyramidal and Mexican Narrow Ear. These varieties likewise show a strong affinity in plant type to certain central Mexican corns. Tassel branches are several and are usually rather short. Leaves are broad and the sheaths often carry strong plant color. The leaf sheaths tightly envelop the culms as contrasted to the loose "puffy" sheaths of the gourdseeds and shoepegs. In the variety Tuxpan, the sheaths above the ears exhibit considerable pubescence both on the backs as well as at the edges, a common characteristic of most varieties of Central Mexico.

C. *Hickory King.*—Hickory King, one of the older varieties of southern dents, possesses a group of ear characteristics that are so distinctive as to make it necessary to place it in a separate category among southern corns. Ears are narrow and cylindrical with 8 to 10 rows of seeds that are often as wide as long. Seeds are strongly flattened on top, and there is a very strong tendency for row pairing. A distinct cap of soft starch with a rather shallow dent and some wrinkling is characteristic of the variety. Plant type in Hickory King is not particularly distinctive. It is similar to many other old southern dents in that the plants are tall, have few tillers, and increasingly short internodes above the ear.

The relationship between Hickory King and certain Mexican corns seems quite clear. There is little doubt that the variety has arisen from a similar group of corns in Mexico that are known as "*tabloncillo.*" They form the commonest varieties of field corn over large areas in western Mexico and belong to the general race of corn termed Mexican Narrow Ear by Anderson (1946).

Derived Southern Dents.—

These corns apparently originated out of mixtures of gourdseeds, shoepegs, semi-hard Mexican June types, tropical flints and cylindrical dents from the corn belt. In ear type some show considerable gourdseed tendency, while others (including many of the "prolifics") appear to be rather closely related to the Mexican June complex. Jarvis Golden Prolific and similar varieties have many

characters in common with Creole or Caribbean flints and may carry rather large amounts of germ-plasm from this or some closely related source. Also among the varieties that we have included with the derived southern dents are those strains which are very similar to corn-belt dents. Perhaps they arose in the southern periphery of the corn belt in the same manner as did most corn-belt corn (i. e. through the union of northern flints and old southern dents) or perhaps they are the result of mixing old or derived southern dents with corn-belt dents.

Importance of the Old Southern Dents for the United States Corn Belt

The old southern dents should be of more than passing interest to corn breeders in that middle-western area centering in Iowa which is known as the United States Corn Belt. In the last few years there has been considerable interest among some United States corn-breeders in the possibility of obtaining superior germ-plasm from maize varieties in Central America and Mexico. Since the old southern dents are so similar to several Mexican types, many of the desired genes might be obtained with far less trouble from certain southern dents than from the Mexican varieties from which they are derived. The fact that they have already been moved part way towards the North should simplify the task of incorporating any of their desired characteristics into corn-belt inbreds. Our preliminary results indicate that the maturity of most southern dents will permit their being used in crosses in the Midwest without resorting to the use of day-length control. Since the general growth habit of southern United States varieties is already fairly similar to northern ones, there probably would be fewer undesirable combinations to be discarded in breeding from southern material.

One specific quality which might prove useful in future breeding programs is the soft texture of the southern dents. Preliminary results indicate that crosses with these southern varieties will produce softer-textured dents than have been available in the corn belt. If changes in the methods of harvesting corn-belt maize should make it desirable to breed for varieties with two or more ears, certain southern varieties of prolific habit could supply the genes necessary for the expression of this character. There are already indications in our data that much of the heterosis in United States corn-belt varieties comes from combining northern flints and the southern dents. It is improbable that the maximum number of genes making for hybrid vigor has already been extracted from these two stocks. It might be possible to increase the potential hybrid vigor of our corn-belt hybrids by bringing deliberately into our inbreds additional sets of differing genes from the northern flints and the southern dents.

One of the most promising uses of the southern dents may be to illuminate the genetics of multiple-factor characters in maize. From the viewpoint either of the practical breeder or of general evolutionary theory, the genes which control multiple-factor differences are of far greater importance than the single genes

ordinarily employed in genetic experiments. Yet in spite of their over-all importance we know little about them, and experiments designed to tell us more have been so discouragingly difficult that little real advance has been made since East's preliminary investigations. A study of the northern flints and southern dents is a promising avenue of approach to this problem. It has been shown from data on species crosses, as well as from theoretical deductions, that in crossing well-differentiated races, all the multiple-factor characters are partly linked in the second generation and that the total effect of this linkage can be removed only by many generations of controlled breeding, if at all. We may therefore expect the multiple-factor characters which differentiate the northern flints from the southern dents still to be somewhat linked in the maize of the United States corn belt. The experience of practical breeders indicates that this expectation is certainly realized. High-row numbers, tapering ears, soft texture, and pointed kernels are characters which went together into corn-belt corn from the southern dents. It is common experience among corn-breeders that this complex of characters still tends to stay together after a century of breeding and selection.

A careful study of the southern dents, particularly in their contrasts to the northern flints, should help us by suggesting character combinations which may still be more or less associated in modern corn-belt varieties. Furthermore, by using corn belt inbreds, northern flints, and southern dents, in controlled experiments, it should eventually be possible to learn what kinds of genes differentiate these types of maize, roughly how many of them there are, and on what chromosomes they are distributed.

Summary

1. The dent corns of the South are of importance because some of them were extensively used during the nineteenth century in developing the more highly derived varieties of the United States corn belt.

2. After several years of preliminary study, a comprehensive collection was assembled and grown in duplicate in Iowa and Missouri. Standardized photographs were made of plants, tassels, and ears. Pachytene smears of the pollen mother cells were studied to determine the number of chromosome knobs. A portion of this information is summarized in tabular form.

3. For the purposes of this discussion the southern dents are roughly grouped into: (1) the old southern dents, and (2) derived southern dents. The former were almost certainly derived from certain Mexican varieties. The derived dents originated from crosses between the old southern dents and northern and tropical flints as well as from crosses with corn-belt dents.

4. No archaeological records of old southern dents or of similar varieties have yet been obtained from the eastern states. Our earliest records are accounts from Louisiana and Virginia in the eighteenth century. The historical evidence for their having been used in the creation of the varieties of the present United

States corn belt is well documented and reasonably complete.

5. The chromosome knob numbers of the old southern dents in our cultures ranged from 4 to 12. As might be expected, numbers were higher among the old southern dents than among the derived dents.

6. The morphology of the southern dent corns is briefly summarized. The more important varieties such as Gourdseed, Shoepeg, and Hickory King, are discussed in more detail.

7. The probable usefulness of the southern dents to practical plant breeding and to theoretical genetics is discussed. It is suggested that they might be more useful sources for certain desirable characters, such as soft texture, than some of the Mexican and Central American varieties which have been considered. To theoretical genetics, they offer a combination of multiple-factor characters which is greatly different from that found in modern United States corn and still more radically different from that of the northern flints. By intercrossing these three types of corn (and with the use of marker genes and cytological analyses) it should be possible to estimate the numbers of multiple-factor genes involved and their distribution in the germ-plasm.

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Explanation of Plates

PLATES 18–23

Representative specimens of "old" and "derived" varieties of southern dent corns; 1—plant; 2—mature tassel; 3—typical ears; 4—seeds. Each division on the background of plant and tassel photographs represents 50 (cm.). Each division on the scale opposite the ears represents 1 (cm.).

Plate 18. Caraway's' Prolific.

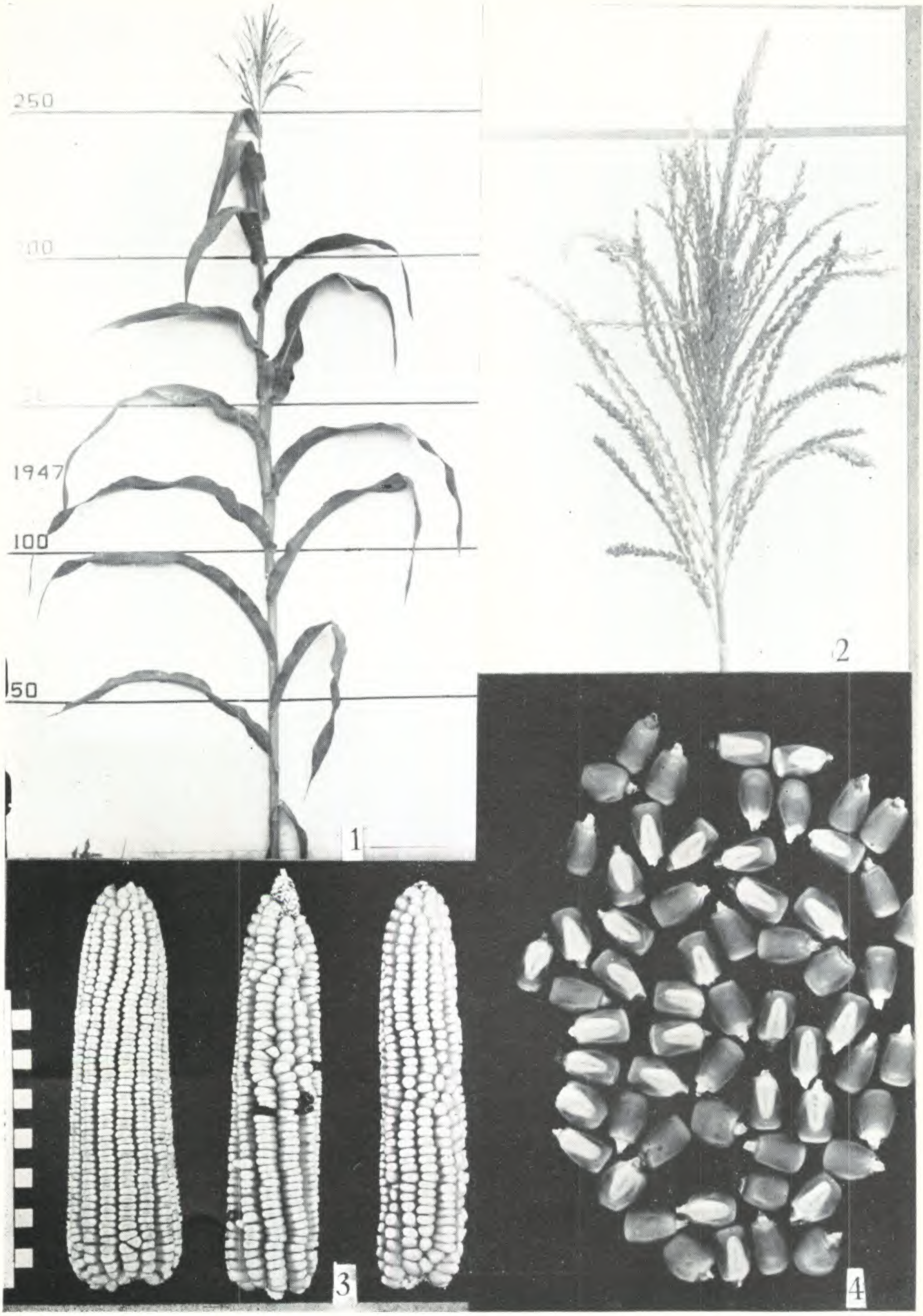
Plate 19. Tuxpan.

Plate 20. Gourdseed.

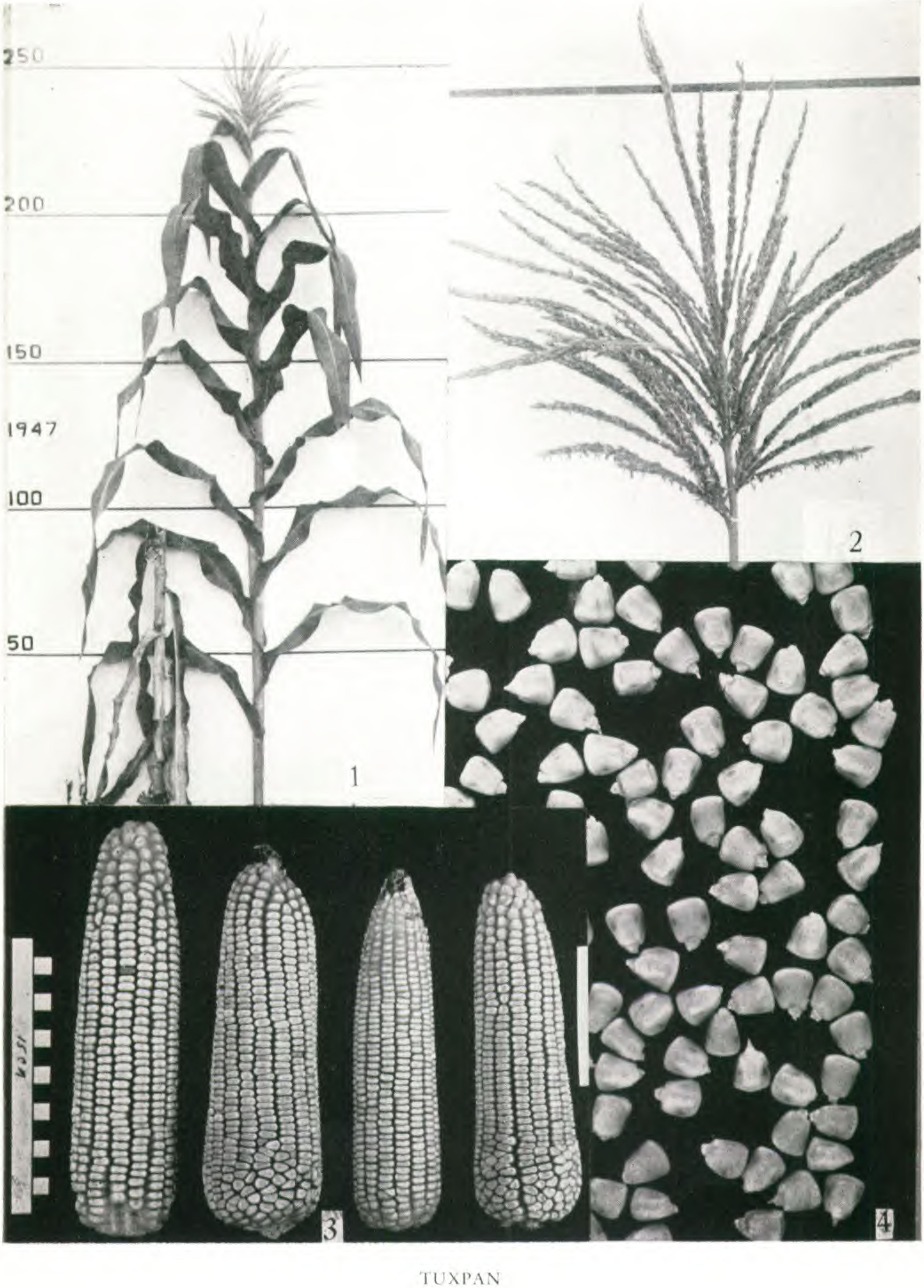
Plate 21. Shoepeg.

Plate 22. Mexican June.

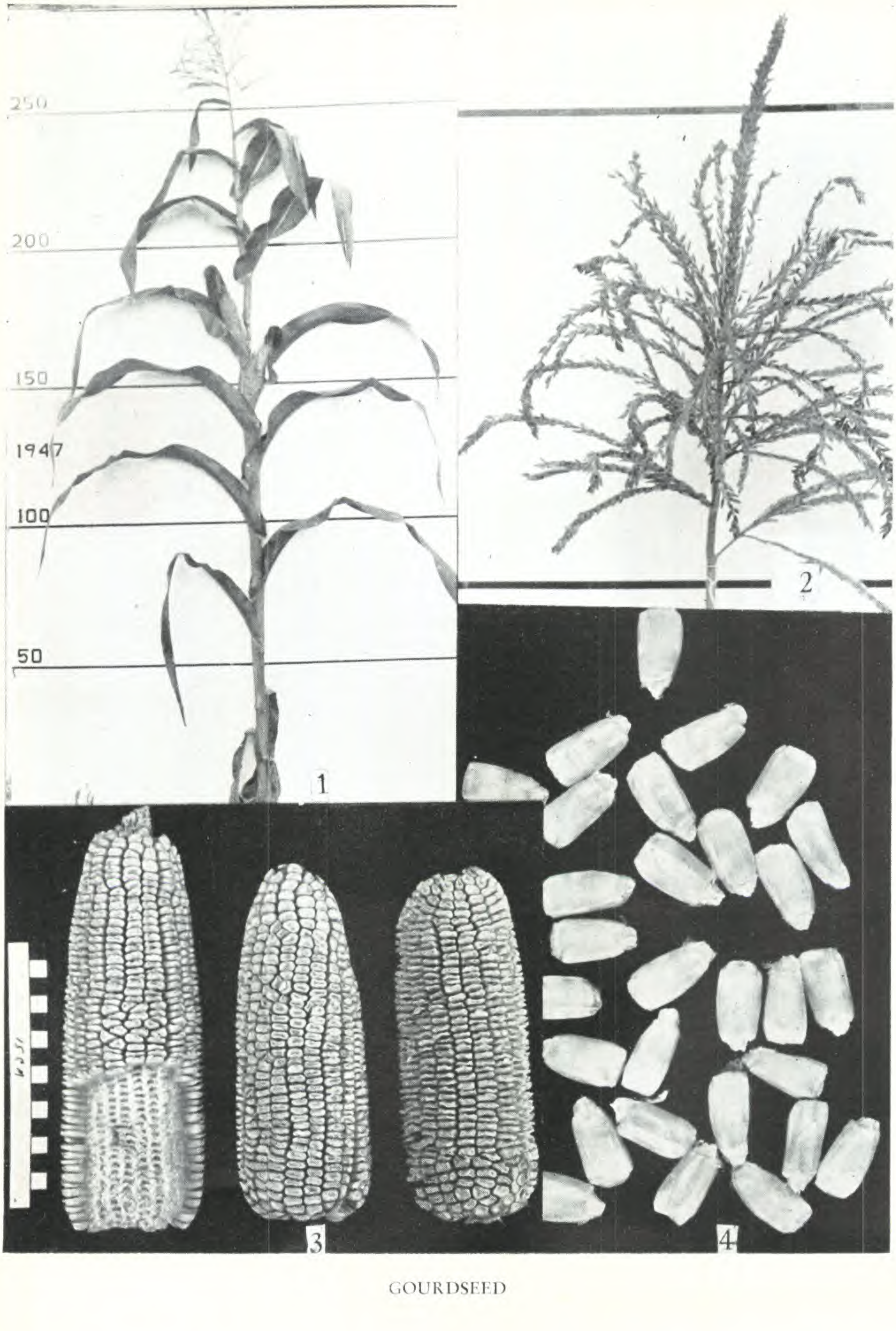
Plate 23. Hickory King.



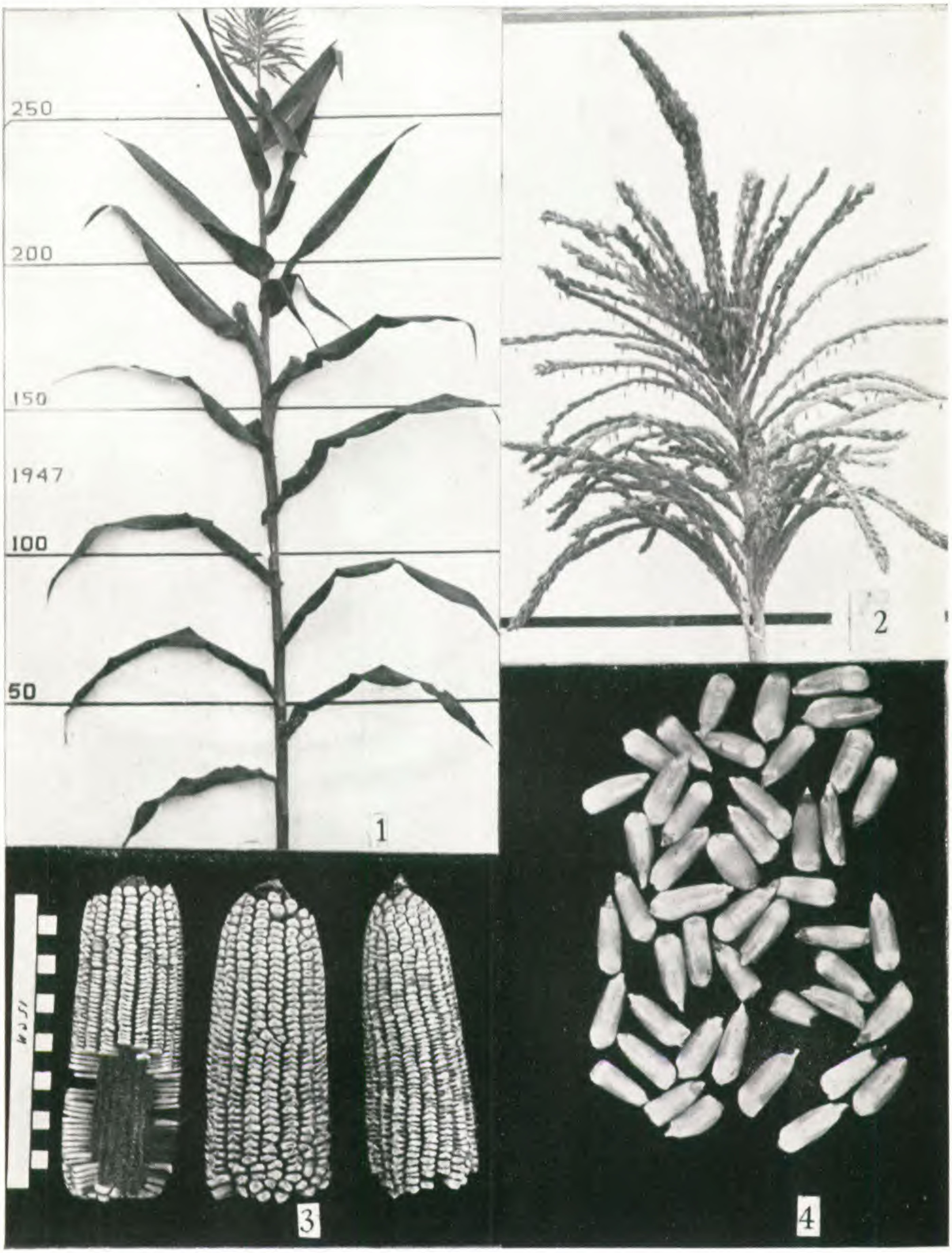
CARAWAY'S PROLIFIC



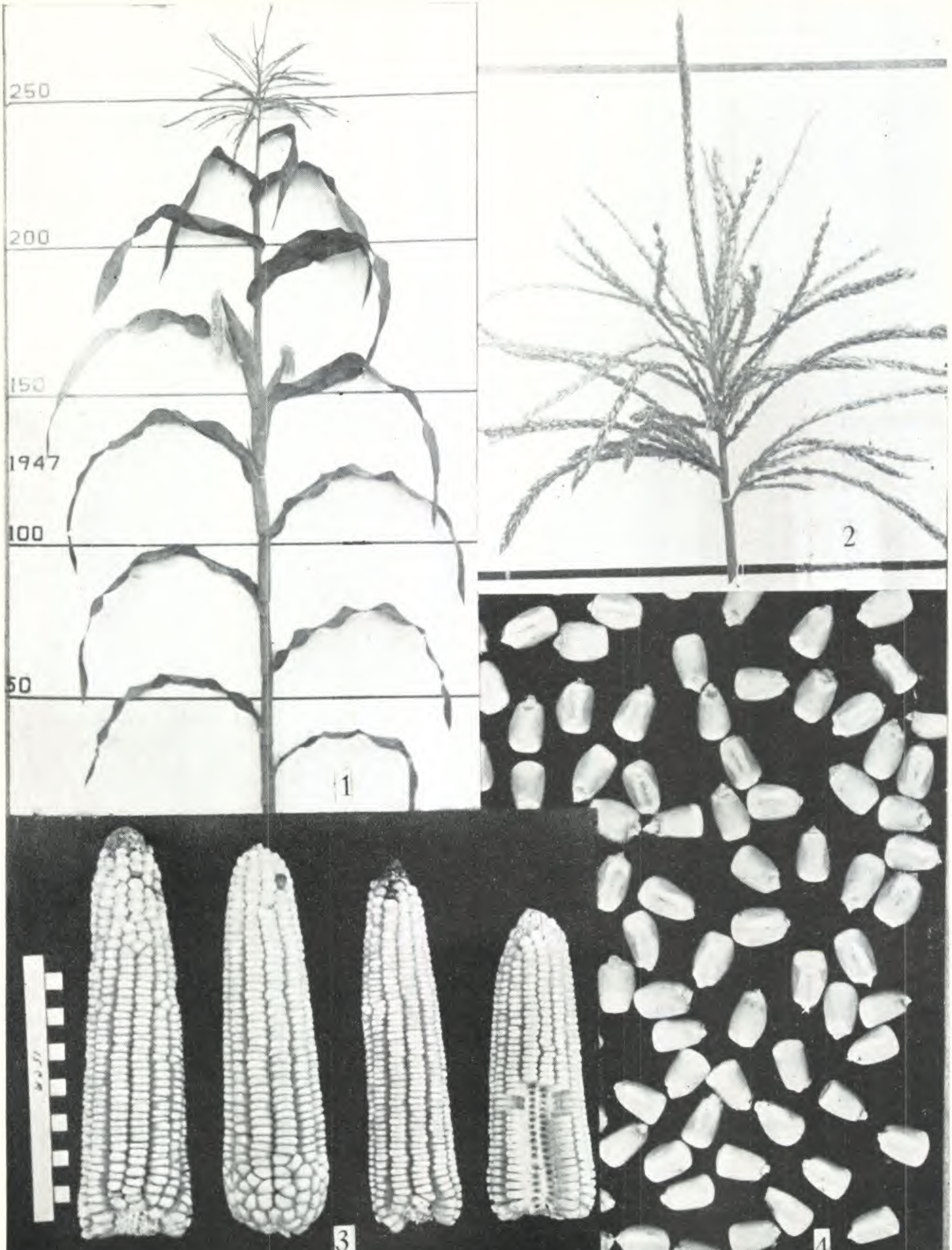
TUXPAN



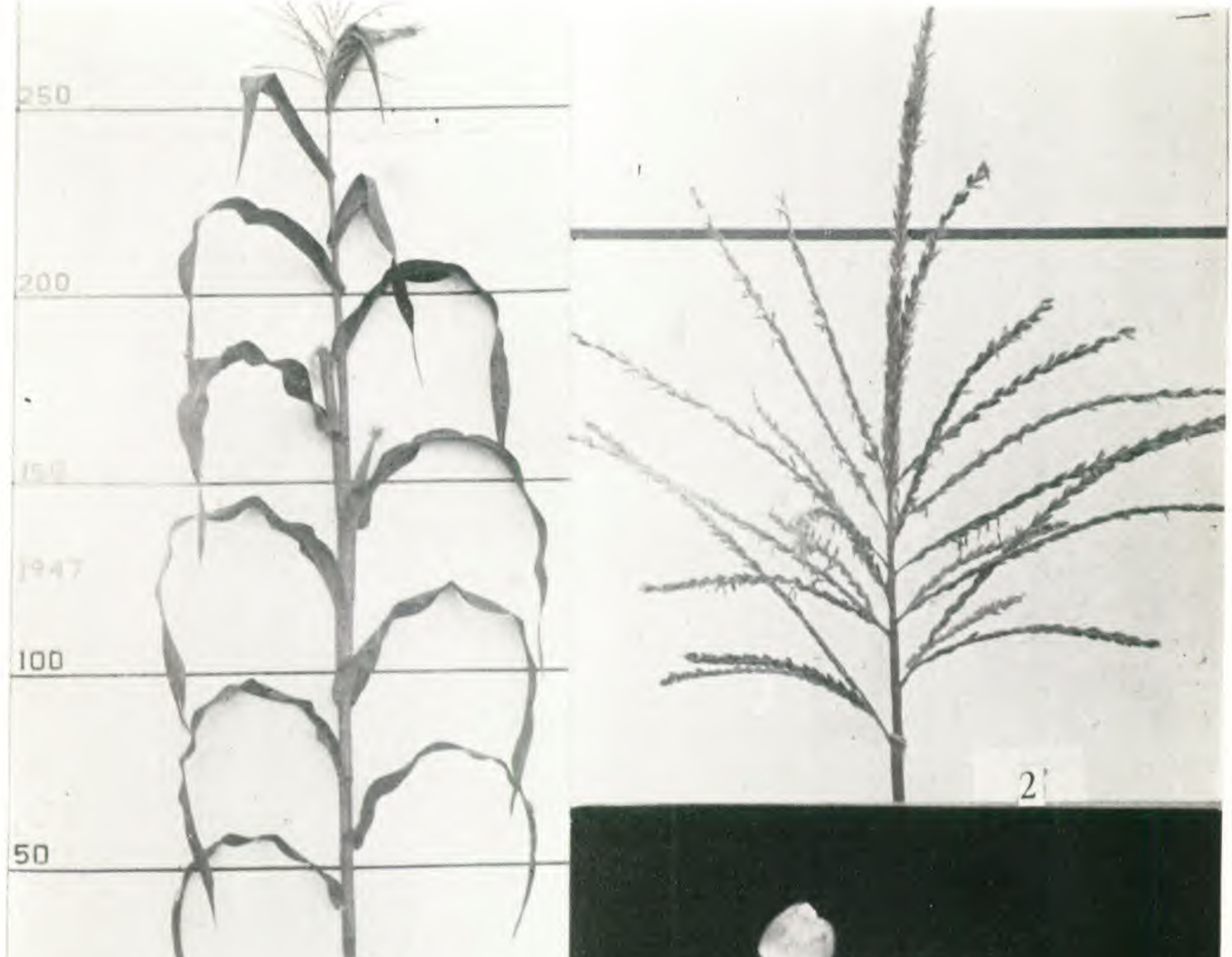
GOURDSEED



SHOEPEG



MEXICAN JUNE



HICKORY KING

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EAR AND TASSEL DEVELOPMENT IN MAIZE

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A study of the changes that take place in the growing points which form the ear and tassel of maize, or Indian corn, reveals a number of relationships that cannot be seen in the mature plant. It shows how the parts of the ear and tassel are formed from the growing point; where the parts are placed in relation to each other; and the sequence of the differentiation of the parts. Such a study is focused on the beginning rather than on the end of the developmental cycle and as a consequence a better understanding can be attained of variations in certain characteristics such as ear row number, ear height, time of sexual maturity, and of certain correlations in the development of the tassel and ear.

This paper will be limited to a description of the differentiation and development of the ear and tassel of the corn plant. Normal development will be emphasized; however, a description of certain abnormal ear types will be included. Part of the photomicrographs were published earlier (Bonnett, 1940) and are used again in this paper because they show clearly the various developmental stages of the ear and tassel and their parts. The descriptions of these illustrations have been revised.

LITERATURE REVIEW

Certain authors have made extensive reviews of the literature on the morphology of corn and other grasses. Literature on the general morphology of the corn plant has been reviewed by Weatherwax (1916, 1917, 1925), Miller (1919), Arber (1934), and Randolph (1936). Evans and Grover (1940) have a good literature review on the morphology of grasses.

The general morphology of the tassel and ear of the corn plant has been described by Collins (1919), Weatherwax (1916, 1917, 1925), and Arber (1934). Pistillate spikelet development was clearly described by Miller (1919). Randolph (1936) described the development of the caryopsis as well as the pistillate spikelet.

Few studies of the early stages in the development of the ear and tassel of corn have been published. Noguchi (1929) described some of the beginning stages in the development of the ear and tassel. Development of the ear and certain of its characteristics were described by Fujita (1939). A detailed description of the development of the ear and tassel, illustrated by photomicrographs, was published by Bonnett (1940).

Publications dealing with corn morphology from certain specific viewpoints should also be mentioned. A paper by Anderson (1944) on the homologies of the ear and tassel is of value to both the corn breeder and the student of corn morphology. Mangelsdorf has brought together the pertinent information on the morphology of the ear as it is related to the question of the origin and nature of the corn ear. A paper by Cutler (1946) and one by Brown and Anderson (1947) describe morphological details of the ear and tassel of special types of corn.

MATERIALS AND METHODS

First-generation hybrid plants, Golden Cross Bantam (Purdue Bantam 39 $\times$ Purdue 51) and a Country Gentleman hybrid (Illinois 8 $\times$ Illinois 6) sweet corn, were used in working out the details of tassel and ear development. Plants of first-generation hybrids are genetically alike and variation among individual plants is slight, which makes it easier to follow the developmental sequences. The sweet corn plants were grown in the greenhouse in two-gallon jars. Plants of the other ear types were grown in the field.

Seed of the various ear types was obtained from different sources. The Maize Genetics Cooperation, Cornell University, Ithaca, N. Y., furnished seed of 4-row and ramosa. Seed of Longfellow flint and Japanese Hull-less came from William L. Brown, Pioneer Hi-Bred Corn Company, Johnston, Ia. R. R. St. John, DeKalb Hybrid Seed Company, Champaign, Ill., supplied seed of Mexican Long Kernel.

Most of the photomicrographs were taken of living material which was handled as was described by Bonnett (1940). However, tassels and ears of the different ear types were killed and fixed in a formalin—acetic acid—alcohol solution and later dissected and photographed.

PLANT DEVELOPMENT

The beginning of the differentiation of the tassel can be approximately determined by counting the number of leaves or by examining the base of the plant to see if internode elongation has begun (pl. 31). Leaf number is less reliable owing to the fact that early types have fewer leaves than late ones at the time tassel differentiation begins and to the effect of the environment upon the relation between leaf number and tassel differentiation. Beginning of internode elongation has been found to be associated with the beginning of tassel differentiation (pl. 31). However, when it can be determined from an external examination of the plant that the basal internodes are elongating, the earliest stages of tassel development have usually been completed. The only reliable method of determining when tassel development begins is to dissect the growing point of the main shoot and

look at it with a dissecting microscope. If sampling begins early enough and is done at frequent intervals the beginning of tassel development can be accurately determined.

Initiation of ear development is behind the initiation of tassel differentiation. Silking may be synchronized with shedding or it may be ahead of or after pollen shedding on the same plant. Silking date and its synchronization with pollen shedding varies with the variety and with growing conditions.

TASSEL AND STAMINATE SPIKELET DEVELOPMENT

The shoot of the corn plant, like that of other cereals (Bonnett, 1935, 1936, 1937, 1940) and grasses (Evans and Grover, 1940; and Weber, 1938, 1939), passes through two stages in its development from germination to the dehiscence of the anthers. During the first stage, leaf fundaments, leaves, and axillary shoots are produced and the internodes of the stem remain short. During the second stage the internodes of the stem elongate, the tassel and its parts differentiate and develop, and the axillary shoot or shoots (ear or sucker) pass through their various stages of development.

Two growing points (pl. 24, A and B) represent the appearance of the shoot in the first stage of development. The growing point (pl. 24, A, *gp*) is partly enclosed by two leaf initials. At this stage of development the growing point is much smaller in relation to the diameter of the stem than the growing point of either wheat, oats, or barley at a similar stage of development.

Two processes, which occur simultaneously, indicate the beginning of the second stage of development: (1) The internodes of the stem begin to elongate, and (2) the growing point elongates in preparation for the differentiation of the tassel and its parts. Tassel development is completed when the anthers dehisce.

Branch primordia are the first of the tassel parts to differentiate (pl. 24, C, *b*, and D, *b*). They arise in acropetal succession as lateral projections from all sides of the elongated central axis. Some of the branch initials at the base of the central axis elongate and become the lateral axes of the tassel (pl. 24, E, b_1). The other initials arising from a point higher on the central axis are the ones from which the spikelet initials originate (pl. 24, C, *b;* D, *b;* E, *b;* F, *si;* and G, *si*). It should be noted that, in the early stages of tassel development, so far as external appearances indicate, there are no differences between those initials that become the lateral branches of the first order and those from which the spikelet initials differentiate. Therefore, all of the first initials to appear are branch initials.

As has been described for oats (Bonnett, 1937) and grasses (Evans and Grover, 1940), branches of the second order may rise by budding from the base, and at the lateral margins, of the branches of the first order (pl. 24, E, b_2, and K, b_2). It has already been stated for the central axis that those initials of the lateral axes above the most basal ones are the primordia from which the spikelet initials differentiate.

In studies made on barley, wheat, and oats (Bonnett, 1935, 1936, 1937) and grasses (Evans and Grover, 1940), there was always an indication of leaf fundaments on the central axis in the axils of which the lateral shoots of the inflorescence were formed. Although there is no indication of leaf fundaments subtending the initials of the lateral shoots of the tassel of the sweet corn studied, in certain other types of corn they have been found. There are structures apparently homologous with leaf initials, subtending the lateral shoots of the ear (pl. 26, C, *l*).

All the branches of the tassel are indeterminate. Neither the central axis (pl. 24, I, *t*) nor the lateral axes (pl. 24, J, *t*, and K, *t*) of the tassel terminate in apical spikelets. Primordia from which the spikelet initials differentiate are produced acropetally as long as the axes increase in length.

In the beginning of spikelet development the branch initial divides into two unequal parts, the spikelet initials (pl. 24, F, *si;* G, *si;* and H, *si*). The spikelet that develops from the larger spikelet initial is pediceled (pl. 25, E, *s'*) and the one from the smaller initial is sessile (pl. 25, E, *s*). The larger initial is always in advance of the smaller in its development. This is shown by the beginning of development of the empty glume on the larger initial in plate 24, H, *e*, and the lack of such development in the smaller initial, and by the beginning of anther differentiation in the larger spikelet in plate 25, C, *s'*, and the lack of anthers in the smaller spikelet (pl. 25, C, *s*).

Several of the early stages of spikelet development can be seen in plate 24, H, which shows a group of spikelets from the central axis of the tassel. Beginning at the top of the photograph, the developmental stages range from an undifferentiated lateral shoot initial, through the various stages of division into spikelet initials, to the beginning of development of the empty glumes. The empty glumes are the first of the spikelet parts to form and are first seen as transverse ridges across the spikelet initial (pl. 24, H, *e*). They grow in length and finally enclose the flowers (pl. 25, I). Spikelet initials develop from all sides of the central axis of the tassel (pl. 24, G) but only on the abaxial side of the lateral branches. The abaxial side of branches of the first and second order are shown in plate 24, K, b_1, b_2, and the adaxial side of a branch is shown in plate 24, J. Two rows of lateral shoot primordia develop, and they divide into two pairs of spikelet initials.

At any stage of development the central axis of the tassel is in advance of the branches (pl. 24, F, L, and M). This is what should be expected since the central axis is formed first and the branches differentiate from it. The branches increase considerably in size before the initials from which the spikelets differentiate are produced.

In each staminate spikelet two flowers develop from the meristem located above the empty glume initials (pl. 24, H, *gp'*). The meristem divides into two unequal parts. The larger part gives rise to the upper flower (pl. 25, A, fl_1, and B, fl_1) and the smaller part develops into the lower flower (pl. 25, A, fl_2, and B, fl_2). These flowers differ in their rates of development. The anthers of the upper flower (pl. 25, A, fl_1; B, fl_1; D, fl_1; and G, fl_1) differentiate first, and

their development is always ahead of the corresponding parts of the lower flower (pl. 25, A, fl_2; B, fl_2; D, fl_2; and G, fl_2). As the flowers approach maturity the anthers of the lower flower attain nearly the same size as those of the upper flower (pl. 25, G, fl_1, and fl_2).

Anther initials are the first of the flower parts to differentiate (pl. 25, A, *an,* and B, *an*). Since the tassel flowers are staminate, anther differentiation and development are the principal growth activities within the flower. Pistils may develop from the meristem located above the anther initials (pl. 25, A, *p*) but they usually remain rudimentary (pl. 25, B, *p*). Under certain conditions of growth the pistil may show considerable development (pl. 25, F, *p*) and may become fully developed and functional. Flowering glumes develop for each flower, but they are so thin (pl. 25, G, *g*) that they are difficult to distinguish at the beginning of their development. The lemma and palea begin their development as thin ridges at a point on the meristem just below the anther initials (pl. 25, B, *g*) at about the same time that the anther initials begin to differentiate.

Deviations from the normal development under field conditions are often seen in plants grown in the greenhouse. Normally one spikelet is sessile and the other pediceled (pl. 25, E), but both spikelets may be sessile (pl. 25, H). Another type of deviation which will be described later is the development of functional pistils in the tassel.

EAR AND PISTILLATE SPIKELET DEVELOPMENT

In the early stages of stem development a shoot is produced in the axil of each leaf, but at a later stage axillary shoots are no longer produced. The cessation of axillary shoot development seems to be associated with the elongation of the internodes of the stem and the development of the tassel.

Ears develop from the upper one or more axillary shoots of the stem. Those shoots, formed at the base of the stem, may remain non-functional or develop into suckers. If an examination is made at the time the topmost shoots are producing ear initials, it will be found that the growing points of the basal shoots are producing only leaf fundaments; but they are more and more advanced in development from the base to the top of the stem. Axillary shoots develop in acropetal succession and during the early stage of stem development they become larger in succession from the apex to the base of the stem. Later, when the ears begin to develop, the size sequence changes, so that the topmost shoot is the largest and the shoots become smaller from the top to the base of the plant. The topmost shoot or the topmost two or three shoots, depending upon whether they are single- or multiple-eared types, in turn take precedence in their development or they may inhibit the development of the shoot immediately below. This difference in development is shown by the size of the ear initials in plate 26, I, J, and K, which are the ear initials from the topmost, second, and third shoots, respectively. The axillary shoot is enclosed in a strongly keeled prophyllum (pl. 26, A, *pr,* and B, *pr*) which may be entire or divided. Leaf initials that develop into husks are covered by the prophyllum.

Ear differentiation is indicated by an elongation of the growing point of the axillary shoot and the differentiation of lateral projections from the central axis of the ear initial (pl. 26, C, and D). The lateral projections are the branch initials from which the spikelet initials differentiate, and correspond to the branch initials that first appear on the central axis and branches of the tassel. Subtending each initial, as has already been mentioned, are ridges (pl. 26, C, *l*) which are similar to the subtending leaf initials that appear in the differentiation of the inflorescences of barley, oats, and wheat. These ridges increase in size and form the cup-like depressions (alveoli) in which the spikelets occur (pl. 28, B, *x*).

Spikelet initials are produced in pairs by the division of the preceding initial into two unequal parts (pl. 26, E, *si*). Thus in the ear there is potentially a pediceled and a sessile spikelet from each branch initial, as in the tassel, although the subsequent development of the spikelets do not seem to bear this out. While the parts of the larger of the pair of spikelet initials begin to differentiate before those of the smaller spikelet initial, the difference in their development is not so great as was pointed out for the spikelet initials of the tassel. The empty glumes are the first of the spikelet parts to form and can be seen as transverse ridges across the spikelet initial (pl. 26, F, *e*, and pl. 27, A, *e*). More advanced stages of development of the glumes are shown in plate 26, G, *e*. As the empty glumes increase in length, they enclose the ovary, but the silk extends beyond them (pl. 27, K, *e*).

The number of rows of kernels per ear is determined by the number of rows of branch initials that differentiate. Each branch initial divides into two spikelet initials and each spikelet initial has one fertile flower in which a kernel is produced. This pattern of development results in an even number of rows of kernels. However, row number is actually determined by the number of rows of branch initials (pl. 26, E) that are produced on the ear initial.

Straightness of the rows of kernels has been shown to be related to the number of rows of branch initials on the ear (Fujita, 1939). If the number of rows of branch initials is even, 4, 6, 8, etc., resulting in 8, 12, 16, etc. rows of kernels, the rows will be straight, making a balanced, symmetrical ear (Mangelsdorf, 1945). If the number of branch initials is odd, 3, 5, 7, etc., resulting in 6, 10, 14, etc. rows of kernels, the rows will be twisted, making an unbalanced, asymmetrical ear. Mangelsdorf (1945) has pointed out that this relationship applies to North American and other varieties of corn which have *Tripsacum* contamination but in Bolivian and Peruvian corn, the twisted-row character is usually independent of row number.

The ear, as well as the tassel, is indeterminate in its growth and continues to elongate at the tip (pl. 26, H, *t*), but many of the flowers at the tip of the ear remain rudimentary (pl. 28, C, *t*). Since the spikelets arise in acropetal succession they are successively younger from the base to the tip of the ear (pl. 26, G and H).

Two flower initials are produced in each spikelet, but in most corn varieties only one flower is functional. In a few types like Country Gentleman sweet corn both flowers are functional.

The two flowers of the ear develop from an unequal division of the meristem of the spikelet just as was pointed out for the flowers of the tassel. The flower differentiating from the larger mass of meristem (the upper flower) takes precedence in its development over the one from the smaller mass of meristem (the lower flower). The larger flower is the functional flower in those types of corn that have only one functional pistillate flower per spikelet. In the types of corn having two functional pistillate flowers per spikelet, the larger flower is more advanced at every stage in its development than the smaller flower.

Anther initials are the first of the reproductive parts of the flower to differentiate (pl. 27, B, *an*). In the pistillate flower the anthers begin differentiation but usually remain small and non-functional. Under certain growth conditions and in the genetic-type anther ear, the anthers of the pistillate flower may attain full development. Anthers well enough developed to show the locules are shown in plate 27, G, *an,* and J, *an.*

The pistil initial develops from the apex of the growing point which is located between the anther initials (pl. 27, B, *p,* and I, *p*). Development begins with the formation of a ridge, the silk initial, which partly encircles the tip of the growing point (pl. 27, C, *s,* and D, *s*). The ovule differentiates from the meristem which is partly enclosed by the developing silk initial (pl. 27, C, *ov,* and E, *ov*). The margin of the silk initial grows more rapidly on one side than on the other (pl. 27, E, *s*). Soon two distinct points appear (pl. 27, F and G) which continue to elongate (pl. 27, G and K) and which finally result in the biparted tip of the mature silk (pl. 28, E). Unequal growth rates of the margins of the silk initial result in the development of a tube-like structure partly enclosing the ovule (pl. 27, E, *ov*). The opening above the ovule gradually closes and becomes the stylar canal (pl. 27, G, *sc;* H, *sc;* and K, *sc*). As the silk elongates it becomes covered with hairs, the structure of which has been described by Weatherwax (1917) and Miller (1919). Hairs are just beginning to appear as fine points upon the silk in plate 27, K, *s,* and L, *s,* and they are shown, fully developed, with pollen grains germinating upon them, in plate 28, E, F, and G. The ovary is shown in plate 28, D, *o,* with the silk attached and partly enclosed by the flowering glumes. At this stage of pistil development all of the external parts have differentiated but the pistil has not attained full size. Silks begin to develop first at the base of the ear (pl. 28, A), and at the later stages of ear development a marked contrast in the length of the silks at the tip and the base of the ear can be seen (pl. 28, C).

An enlargement of a section of the ear at the same stage of development as in plate 28, A, is shown in plate 28, B, in which the attachment of the spikelets, variation in the length of the silks, and the size of the stylar canal can all be seen.

Very soon after pollen grains lodge upon the silk they germinate, and the pollen tube grows down the hair into the silk (pl. 28, F and G). This process has been described by Miller (1919) and Randolph (1936).

DEVIATIONS FROM NORMAL FLOWER DEVELOPMENT

Two deviations from normal flower development will be illustrated and described. The first is the development of two fertile flowers in a pistillate spikelet and the second is the development of pistillate spikelets in the tassel. Illustrations for the first deviation were taken from Country Gentleman sweet corn and are shown in plate 27, I, J, L, and M. Illustrations for the second deviation were taken from Golden Cross Bantam and are shown in plate 29.

It will be recalled that in those types of corn that have only one fertile flower per spikelet, the sterile flower begins but does not complete its development. The sterile flower develops from the smaller of the two divisions of the growing point of the spikelet initial. Anther initials and the pistil initial of the sterile flower differentiate (pl. 27, G, fl_2) but do not complete their development (pl. 27, H, fl_2). The pistil of the fertile flower develops as has been described, but the anthers do not, so that in examining a spikelet of the ear of those types of corn having one fertile flower per spikelet, all that can be seen after the silk has begun to elongate are the empty glumes (pl. 27, K, *e*) and the silk of the fertile flower extending beyond them (pl. 27, K, *s*).

When two fertile flowers develop in a pistillate spikelet each flower goes through the same sequence of development that has been described, but the rates of development are different. The upper flower arising from the larger of the two divisions of the growing point develops more rapidly than the lower flower. This was also pointed out for the development of the two flowers of the spikelet in the tassel. The differences in rates of development of the upper and lower flowers can be seen by comparing the upper flower in plate 27 (I, fl_1; J, fl_1; L, fl_1; and M, fl_1), with the lower flower (fl_2). While the upper flower develops first, the lower flower gradually overtakes the upper flower as the ear approaches maturity, but a difference in the development of the silks persists so that the silks of the two flowers do not emerge at the same time.

Paired grains of corn result when two fertile flowers are produced per spikelet. The germ of the upper flower faces the tip of the ear and the germ of the lower flower faces the base of the ear, resulting in the kernels being placed back to back. With the development of two grains per spikelet the kernels may be crowded out of line so that there are irregular rows or a lack of rows as shown in Country Gentleman sweet corn. Development of paired grains, according to Randolph (1936), was first described in pod corn by Sturtevant (1894), and Kempton (1913) was the first to interpret correctly the development of paired grains as being the result of the development of two fertile flowers per spikelet. Weatherwax (1925), Stratton (1923), and others have also described the development of double kernels.

The development of pistillate spikelets in the tassel is an interesting deviation from normal development. Kempton (1913) has pointed out that if there are pistillate flowers in the staminate inflorescence, it is the upper flower of the sessile

spikelet that is pistillate and both of the flowers of the pediceled spikelet are staminate (pl. 29, A). Spikelet differentiation and the first stages in the development of the flowers are the same in both the staminate and the pistillate spikelets of the tassel. The essential difference lies in the degree of development of the anthers and pistils. In the pistillate flowers both the anthers and the pistil differentiate but the pistil takes precedence in development; in the staminate flowers both the anthers and pistil differentiate but the anthers develop instead of the pistil.

In most corn varieties only one flower, the upper one, of the spikelets of the ear is fertile, and the same is true of the pistillate spikelet produced in the tassel (pl. 29, B). Consistent with the development of the flowers of the ear of this type, the upper flower (pl. 29, A, fl_1, and C, fl_1) developed and the lower flower was abortive (pl. 29, A, fl_2, and C, fl_2). Pistil differentiation and development were the same as previously described for the pistillate flower of the ear. The various stages in the development of the silk are shown in plate 29, A, *s*, to F, *s*, inclusive, and it can be seen that they are essentially the same as already described.

The development of the flowers of the staminate spikelet shows no deviation from normal development except that the pistil is a little further developed than in the tassels having only staminate spikelets. But the example shown in plate 29, A, *x*, should not, perhaps, be considered as typical because even in those plants that did not have pistillate spikelets, a considerably greater degree of pistil development was noted (pl. 25, F, *p*, and H, *p*) than would be expected in plants grown in the field. However, this is what should be expected of corn plants grown in the greenhouse under certain conditions of temperature and light.

EAR TYPES

Tassels and ears of four different ear types at early stages in their development are shown in plate 30. They are: four-row, Longfellow flint, ramosa or branched ear, and fasciated. These ear types are of interest because they deviate from the normal ear type of commercial corn.

In corn with four-rowed ears the spikelets on the central axis of the tassel and on the ear are in two ranks (pl. 30, D and H). The tissue between the ranks of spikelets develops into the cob. Ears of the four-rowed type used in this study varied (pl. 30, E) in the number of rows of spikelets per rank and sometimes there was a mixture of two and three rows of spikelets in the same rank. Some of the four-rowed plants developed four ranks of spikelets. They were eight-rowed like Longfellow flint.

The spikelets on the ear and central axis of the tassel of Longfellow flint are in four ranks (pl. 30, A, B). This gives the ear or tassel, in its early stages of development, the appearance of being square. The ear and central axis of the tassel are long, slender, and sharply pointed at the tip. The four-ranked appearance of the central axis of the tassel and of the ear is the result of the position of the spikelets (Brown and Anderson, 1947). In the tassel there are two pairs of spikelets opposite each other at a node. At any node the spikelets are at right

angles to the spikelets immediately below and immediately above and this arrangement gives the four-ranked appearance.

A ramosa ear resembles a tassel in all of its morphological characteristics (pl. 30, I, J). It has a central axis and lateral branches arising from it. Collins (1917) has described how the ramosa tassel differs from that of normal corn, as follows: "In the Z. *ramosa* tassel the branches are more numerous and gradually decrease in size from the base upward, the transition from branches to pairs of spikelets being imperceptibly gradual." The same is true for the ear as can be seen in plate 30, I and J. In Z. *ramosa* the homology between the ear and tassel can be clearly seen because of the branching of both of the inflorescences. In normal corn, branching in the ear is suppressed but the tassel branches and therefore the ear and the tassel do not appear to be homologous.

Two fasciated types are shown in plate 30, Japanese Hull-less, and Mexican Long Kernel. At this stage of development, the ear and central axis of the tassel are short, thick, and blunt at the tip (pl. 30, C, F, and G). The similarity in the form of the central axis of the tassel and ear is clearly seen at this stage of development of Japanese Hull-less. The Mexican Long Kernel ear has a triparted tip. Other types of fasciated ears may be bi-parted, hollowed out, or flattened at the tip.

Anderson (1944) pointed out the correlation between condensation of the spikelets in the basalmost branch of the tassel and row number of the ear. He also stated that there is a correlation between the portion of the tassel branch that is condensed and the type of fasciation in the ear and the part of the ear that will be fasciated. The tassel of Japanese Hull-less illustrated here is too young to show this correlation. Older tassels of other fasciated types have been studied and they do show condensation of the spikelets. At very early stages of tassel and ear development the short, thick, blunt axis is a good indication of fasciation, and also of a high kernel row number.

SUMMARY

1. The developmental morphology of the tassel, ear, and their parts was studied by dissecting them from the corn plant at different stages in their development. Photomicrographs were taken of the various stages.
2. From germination to the dehiscence of the anthers, the shoot of the corn plant passes through two stages of development. In the first stage, leaves and axillary shoots are produced and the growing points of the main stem and axillary shoots remain short and shaped like a half sphere. In the second stage the growing points of the shoots and the internodes elongate and the tassel, ear, and their parts differentiate and develop.
3. Tassel and ear differentiation begins with the appearance of lateral projections, branch initials, which arise acropetally from the growing points. The branch initials at the base of the tassel elongate but the remainder on the central axis of the tassel and those which arise on the tassel branches differentiate into spikelet initials. All the branch initials of the ear of normal corn remain short

and differentiate into spikelet initials. Ramosa ear behaves like a tassel.

4. In both the tassel and ear the spikelet-forming branch initials divide into two unequal parts to form the spikelet initials which in turn divide into two unequal parts to form the flower initials. In the tassel the spikelet developing from the larger initial is pediceled and is ahead in development of the spikelet developing from the smaller initial, which is sessile. Likewise, the upper flower developing from the larger division of the pistillate spikelet is ahead of and larger than the lower flower developing from the smaller division of the pistillate spikelet.
5. In the ear the difference in the size of the spikelets arising from the unequal division of the branch initial is not so marked as in the tassel. The flower developing from the larger, upper division of the spikelet is the fertile flower, and the smaller, lower division is the abortive flower in those types of corn having only one fertile flower per spikelet. In those types of corn having two fertile flowers per spikelet the upper flower is larger and ahead of the lower flower in development.
6. Flower parts differentiate in the following order: empty glumes, flowering glumes, anthers, and pistil. In the pistil the order of development is ovary, silk, and hairs on the silk.
7. Four-row, ramosa, and fasciated are ear types that differ from the normal, and each type is described.

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Explanation of Plate

PLATE 24

Showing initiation and development of the tassel: *b*, branch initial from which spikelets differentiate; b_1, basal branch of the first order; b_2, branch of the second order; *e*, empty glumes; *gp*, growing point; *gp′*, growing point of the spikelet; *l*, leaf initial; *si*, spikelet initial; *t*, undifferentiated tip of an axis.

A—Growing point of a corn plant having four leaves visible, × 22.

B—Beginning of the elongation of the growing point just before tassel differentiation, × 22.

C and D—Differentiation of the branch initials of the tassel, × 22.

E—Elongation of the basal branches of the tassel, × 22.

F—Beginning of the differentiation of the spikelet initials on the central axis of the tassel, × 22.

G—A stage similar to F with some of the basal branches removed to show spikelet differentiation on the central axis, × 22.

H—Differentiation of spikelets and empty glumes on a portion of the central axis of the tassel, × 35.

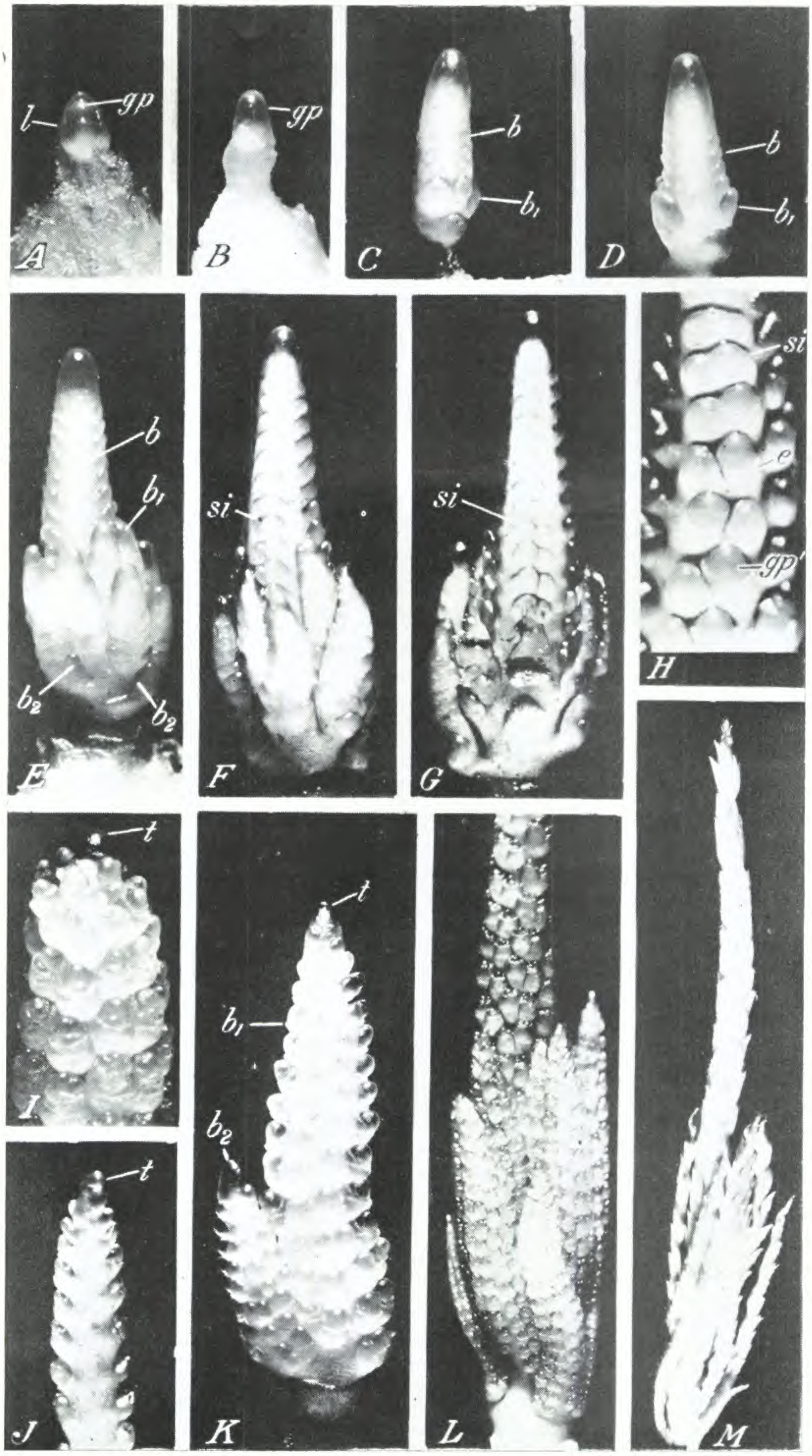
I—Portion of the tip of the central axis of the tassel, × 25.

J—Adaxial side of a branch of the tassel, × 22.

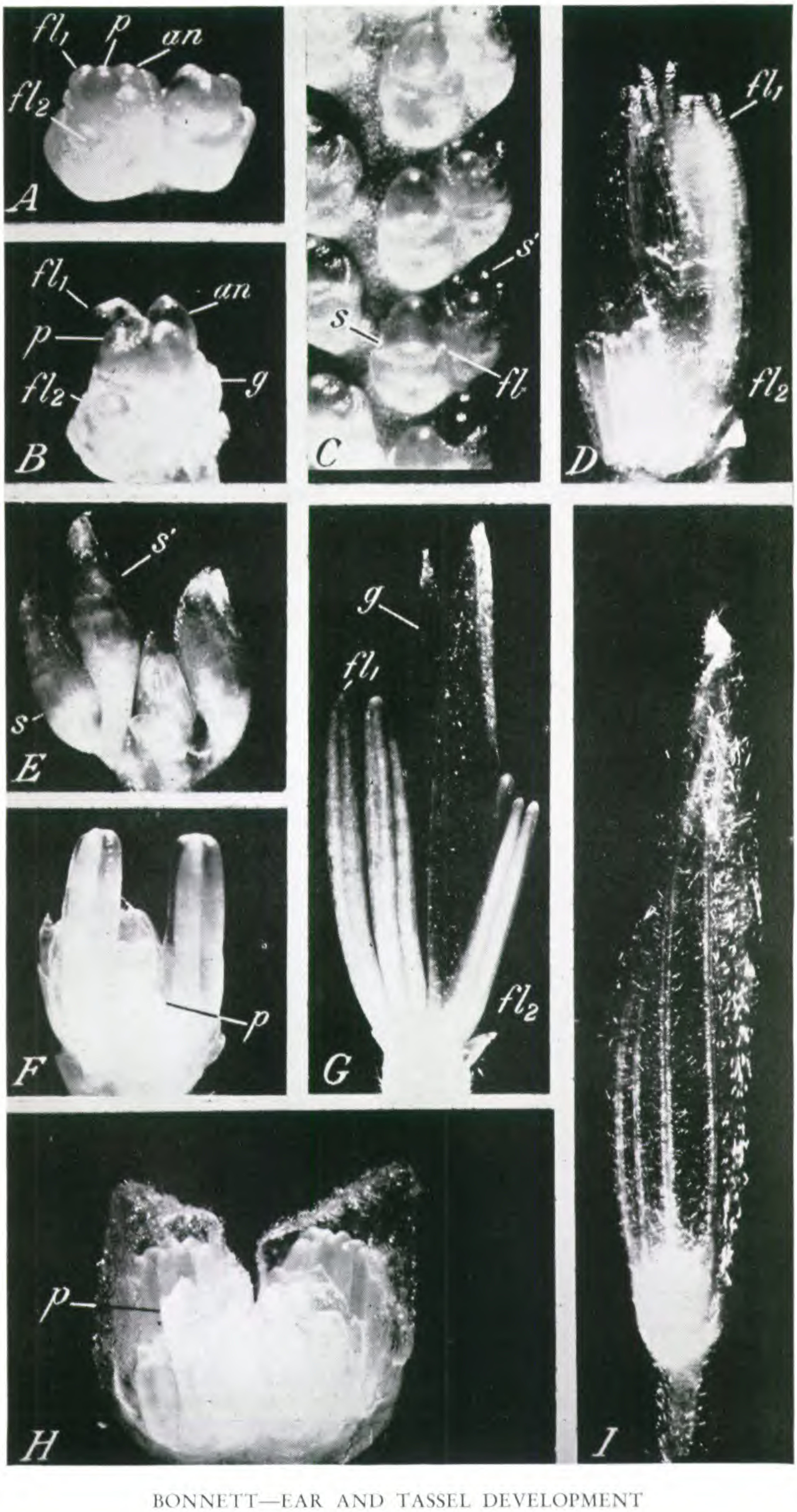
K—Abaxial side of tassel branches of the first and second orders, × 25.

L—A more advanced stage of tassel development, × 22.

M—Fully differentiated but not full-sized tassel, × 8.



BONNETT—EAR AND TASSEL DEVELOPMENT



BONNETT—EAR AND TASSEL DEVELOPMENT

Explanation of Plate

PLATE 25

All figures represent spikelet development in the tassel: *an*, anther; *fl*, flower initial; fl_1, upper flower; fl_2, lower flower; *g*, palea; *p*, pistil; *s*, sessile spikelet; *s'*, pediceled spikelet.

A—A pair of spikelets of the tassel at the beginning of the development of the flower parts. The upper flower, fl_1, is more advanced than fl_2, and the spikelet on the left, pediceled spikelet, is more advanced than the spikelet on the right, sessile spikelet, × 56.

B—Two flowers of a spikelet of the tassel showing the more advanced stage of the upper flower, fl_1.

C—Part of a branch of the tassel showing a more advanced stage of development of the pediceled spikelet, × 40.

D—Staminate spikelet with the empty glumes removed to show the difference in the size of the anthers of the upper and lower flower, × 20.

E—Two pairs of spikelets—one member of each pair is pediceled and the other sessile; the empty glumes have been removed from one spikelet, × 25.

F—Staminate flower with one anther removed to show the partly developed pistil, × 20.

G—Later stage of spikelet development in which the anthers of the lower flower are approaching the size of those of the upper flower, × 10.

H—A pair of spikelets both sessile, × 28.

I—A fully differentiated spikelet, × 10.

Explanation of Plate

PLATE 26

Development of the ear: *b*, branch initial from which spikelet initials differentiate; *e*, empty glumes; *l*, leaf fundament; *pr*, prophyllum; *si*, spikelet initial; *s*, silk initial; *t*, undifferentiated tip of the ear.

A—Axillary shoot in which the ear develops, enclosed in the prophyllum, × 13.

B—Side view of the axillary shoot, × 17.

C—Beginning of the differentiation of the ear, × 25.

D—A more-advanced stage of ear development showing the formation of branch initials, × 25.

E—Beginning of spikelet differentiation by an unequal division of the branch initials, × 22.

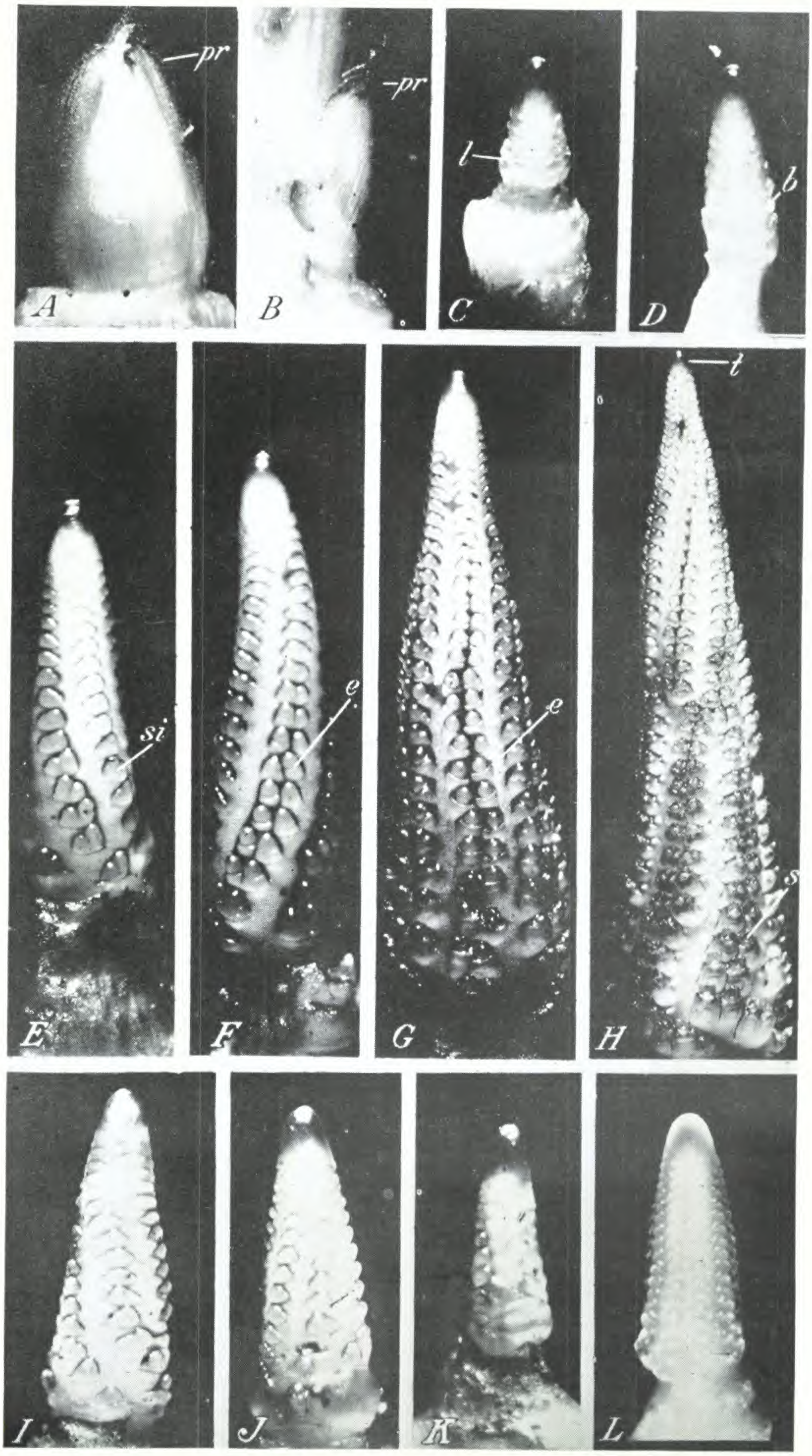
F—Development of the empty glumes as ridges on the growing point, × 22.

G—Paired rows of spikelets of the ear and, a more advanced stage, the development of the empty glumes, × 17.

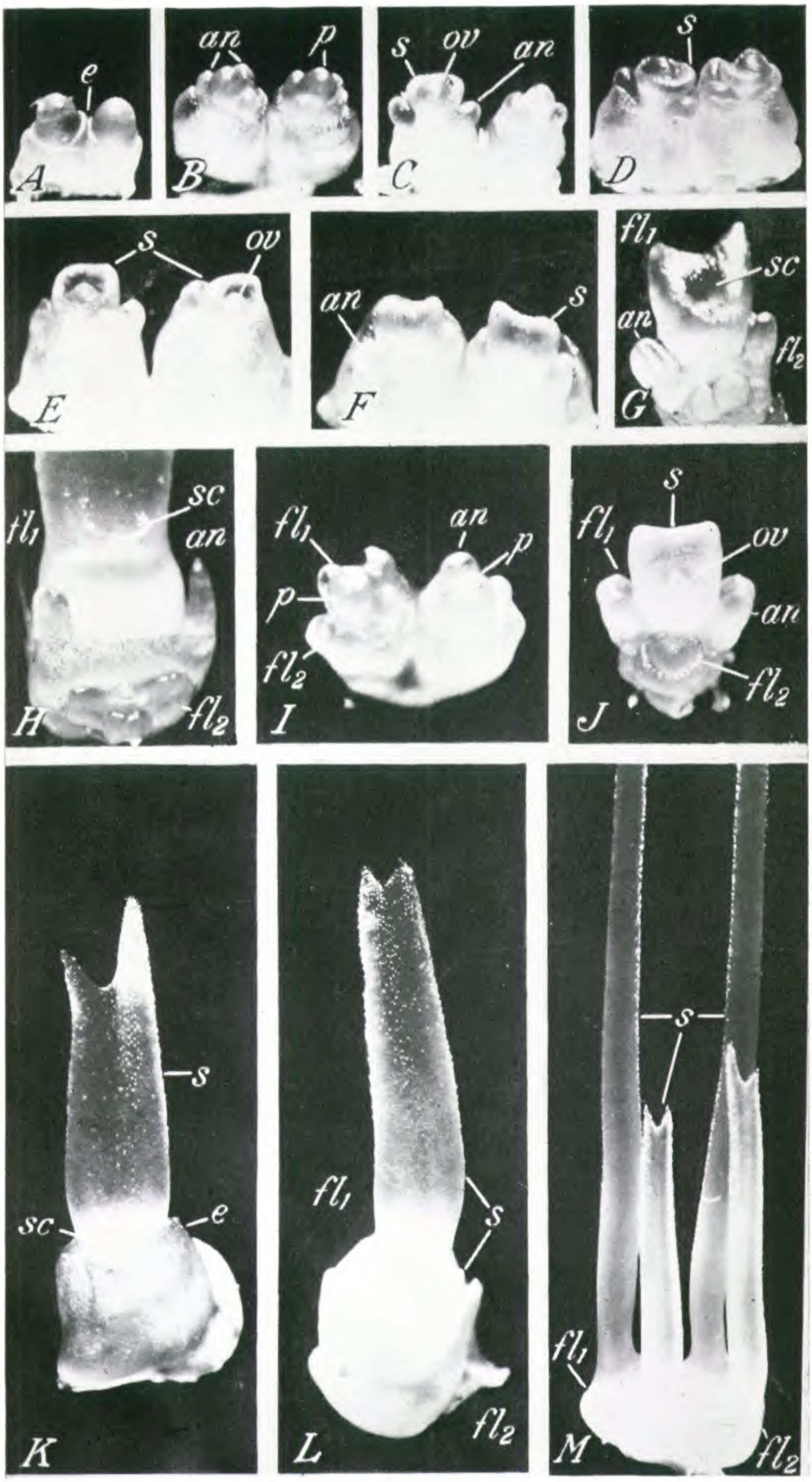
H—The differentiation and development of the silks can be seen at the base of the ear and an irregularity in the rows half way between the tip and butt, × 17.

I, J, and K—Topmost, second and third ears, respectively. All × 22.

L—Young ear of Country Gentleman sweet corn, × 17.



BONNETT—EAR AND TASSEL DEVELOPMENT



BONNETT—EAR AND TASSEL DEVELOPMENT

EXPLANATION OF PLATE

PLATE 27

Differentiation of the pistillate spikelet: *an*, anther initial; *e*, empty glumes; fl_1, upper flower; fl_2, lower flower; *ov*, ovule; *p*, pistil initial; *s*, silk initial; *sc*, stylar canal.

A—Pair of pistillate spikelets at an early stage of development, × 40.

B—Beginning of the differentiation of anthers in the upper flower of a pair of spikelets, × 40.

C—Differentiation of a silk, the first stage of pistil development, × 40.

D—Silk development, × 40.

E—Silks partly enclosing the ovules, × 40.

F—Silk development from the adaxial side, × 40.

G—Spikelet showing the comparative development of the upper and lower flowers, × 40.

H—Functional upper flower and sterile lower flower of a spikelet are illustrated, × 40.

I—Pair of spikelets of Country Gentleman; both flowers are functional, × 40.

J—Spikelet of Country Gentleman; the development of the upper flower is in advance of the lower flower, × 40.

K—Silk development of the functional flower of a spikelet having only one functional flower, × 28.

L—Comparison of the silk development of the lower and upper flowers of a spikelet having two functional flowers, × 28.

M—A more-advanced stage in the development of spikelets having two functional flowers, × 28.

Explanation of Plate

PLATE 28

A—Ear showing different stages of silk development, × 6.5.

B—Section of an ear showing silks at early stages of development and the ridge subtending each spikelet, × 19.

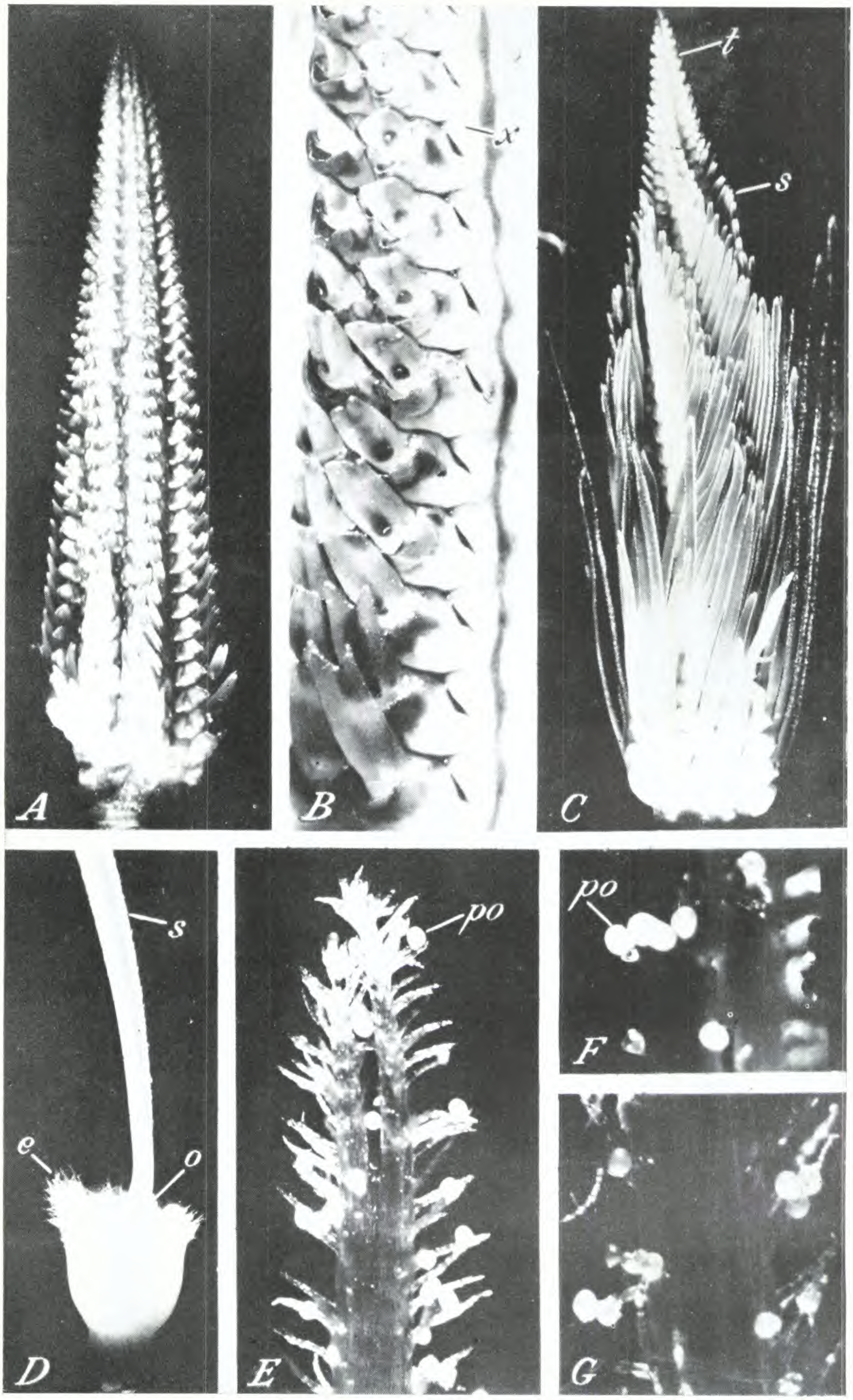
C—Variation in silk development from base to tip of ear, × 6.5.

D—Pistillate spikelet from a tassel, × 14.

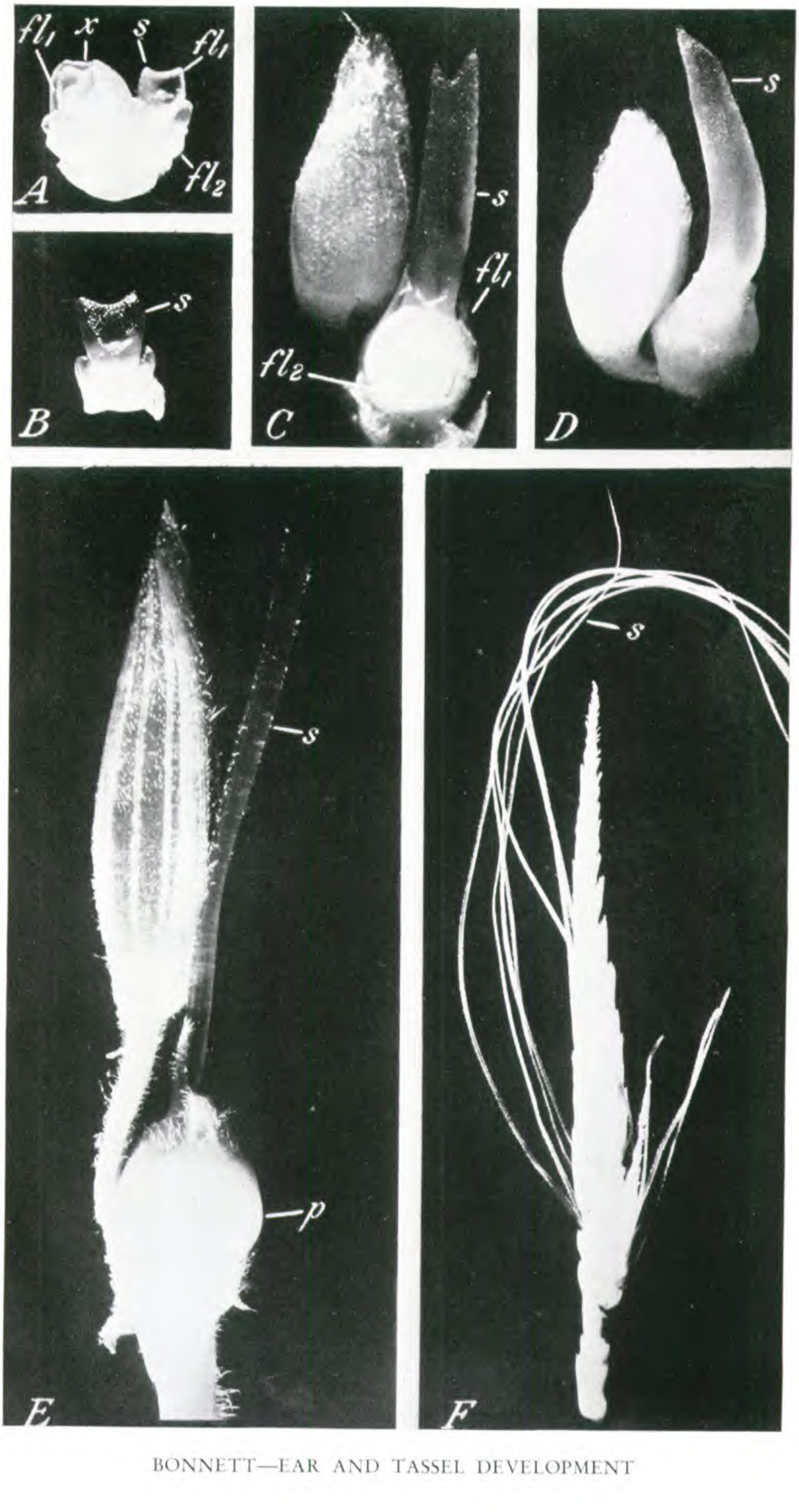
E—Tip of a mature silk with pollen grains germinating on it, × 26.

F and G—Pollen grains germinating on the silk, × 38.

e, empty glumes; *o*, ovary; *po*, pollen grain; *s*, silk; *t*, tip of ear; *x*, ridge subtending the spikelets of the ear.



BONNETT—EAR AND TASSEL DEVELOPMENT



BONNETT—EAR AND TASSEL DEVELOPMENT

Explanation of Plate

PLATE 29

A—A staminate (left) and pistillate (right) spikelet from the tassel, × 20.

B—Silk development in a pistillate spikelet from the tassel, × 28.

C—Glumes removed from the pistillate spikelet to show the abortive lower flower, × 20.

D—Staminate and pistillate spikelets of the tassel, × 15.

E—A fully differentiated staminate, pediceled, and pistillate, sessile, spikelet of the tassel, × 10.

F—A tassel showing silks from the pistillate spikelets at the base of the tassel, × 10.

fl_1, upper flower; fl_2, lower flower; *p*, pistil; *s*, silk; *x*, upper flower of the staminate spikelet.

Explanation of Plate

PLATE 30

A—Tassel of Longfellow flint showing the development of spikelets on the central axis.

B—Ear of Longfellow flint. The arrangement of its eight rows of spikelets gives it the appearance of being square.

C—Ear of fasciated type, American Long Kernel. The tip of the ear is triparted.

D—Tassel of four-rowed corn. The spikelets on the central axis of the tassel are in two ranks.

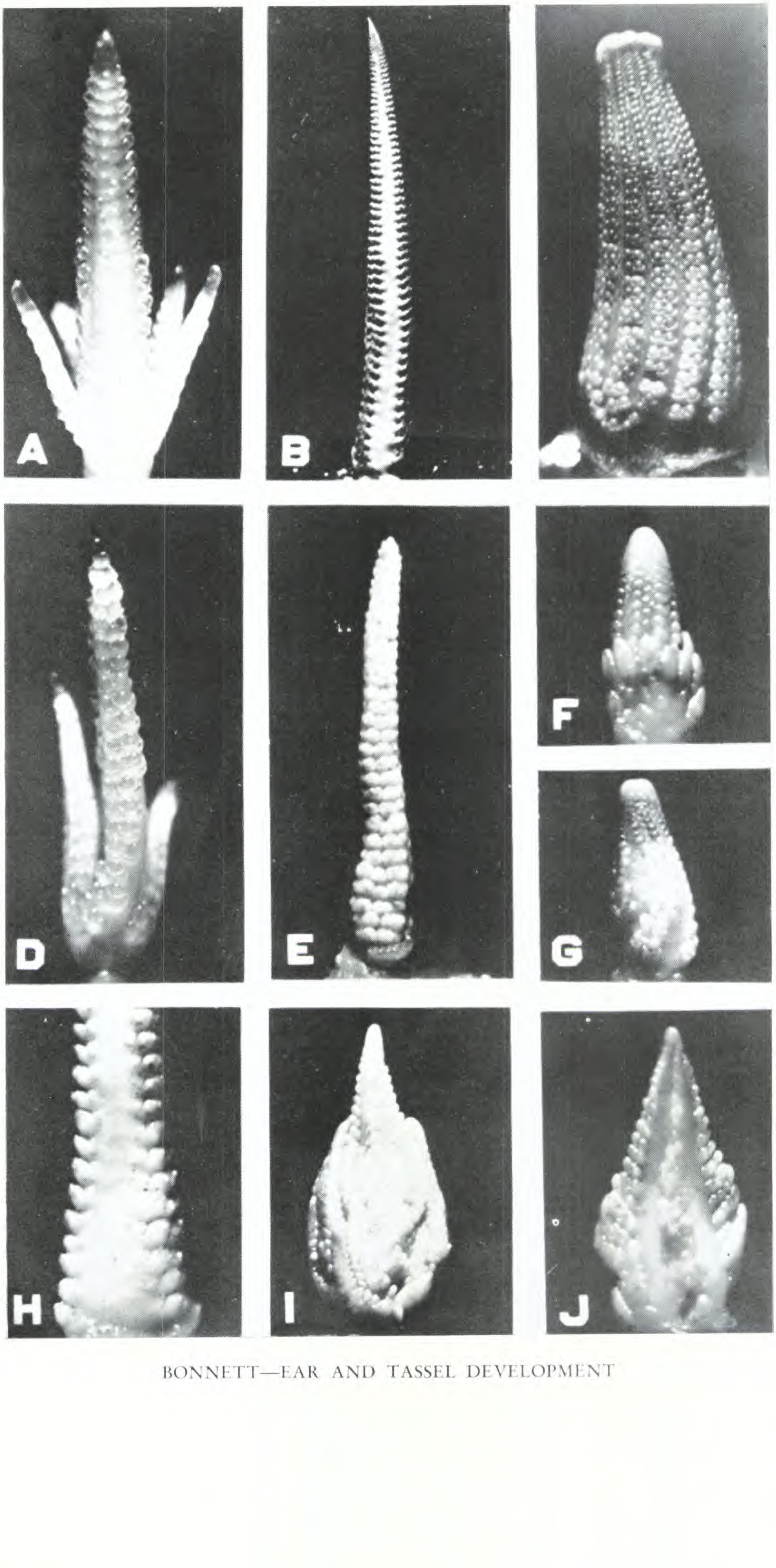
E—Ear of four-rowed corn.

F—Tassel of Japanese Hull-less. The central axis is blunt and thick.

G—Ear of Japanese Hull-less. The characteristics of the ear are similar to those of the central axis of the tassel.

H—Side view of a portion of an ear of four-rowed corn. The spikelets are arranged in two ranks.

I and J—Ears of ramosa or branched-ear corn. Branch elongation is carried well up to the tip of the ear.



BONNETT—EAR AND TASSEL DEVELOPMENT

BONNETT—EAR AND TASSEL DEVELOPMENT

Explanation of Plate

PLATE 31

At the left is a corn plant, and at the right is a plant from which all of the leaves have been removed. The tassel can be seen at the tip of the stem of the stripped plant. Ear shoots are too small to be seen.

A COMPARATIVE DEVELOPMENTAL STUDY OF A DWARF MUTANT IN MAIZE, AND ITS BEARING ON THE INTERPRETATION OF TASSEL AND EAR STRUCTURE

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The homologies of tassel and ear structure in maize, and the problem of the morphological relationship between the inflorescences of maize and other genera in the Gramineae, have provided a fascinating study for many workers. Mangelsdorf (1945) has lately compiled a critical review of the earlier contributions to these problems, and with the aid of more recent data has endeavored to formulate a hypothesis incorporating the main features of previous theories. It is interesting to note that most workers have considered the maize inflorescence (tassel or ear) as a unit for comparative study which is complete in itself. Anderson (1944) first realized the importance of considering the structure of the inflorescence as a culmination of developmental processes which are common to the plant as a whole. It would seem that a study of the inflorescence apart from the rest of the shoot might neglect a very valuable source of information, and that a better understanding of the general developmental plan in the maize plant might furnish a new line of attack in interpreting the particular morphology of the inflorescence.

Adopting this line of approach, the problem of ear and tassel homologies involves three ontogenetic questions:

(1) Bonnett (1940) showed that the primordia giving rise to lateral branches, and the primordia giving rise to paired spikelets on the main axis of the tassel, are homologous structures. Paired spikelets may therefore be regarded as greatly reduced lateral branches. Is this reduction peculiar to the tassel or is it the culmination of a process initiated during the vegetative phase?

(2) Mangelsdorf (1945) concluded that the ear of maize as exemplified by the female inflorescence of Guarany pod corn is "fundamentally identical with the spikes of certain other species of grasses . . . . and like many of them is probably derived from a panicle as the result of reduction of branches. There is not the slightest evidence of fusion." Without in any way disagreeing with the first part of this statement, it may be pointed out that from the developmental point of view the morphology of the panicle represents the crux of the problem; namely, by what developmental process is the simple alternate (distichous) arrangement of primordia, as seen in the basal vegetative portion of the shoot, transformed into the polystichous arrangement found in the apical reproductive region.

(3) Bonnett's developmental studies have shown that the florets of both male and female inflorescences are potentially hermaphrodite. What factors determine

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whether the anthers shall degenerate leaving a pistillate inflorescence in the ear, or the pistil degenerate leaving functionally male flowers in the tassel?

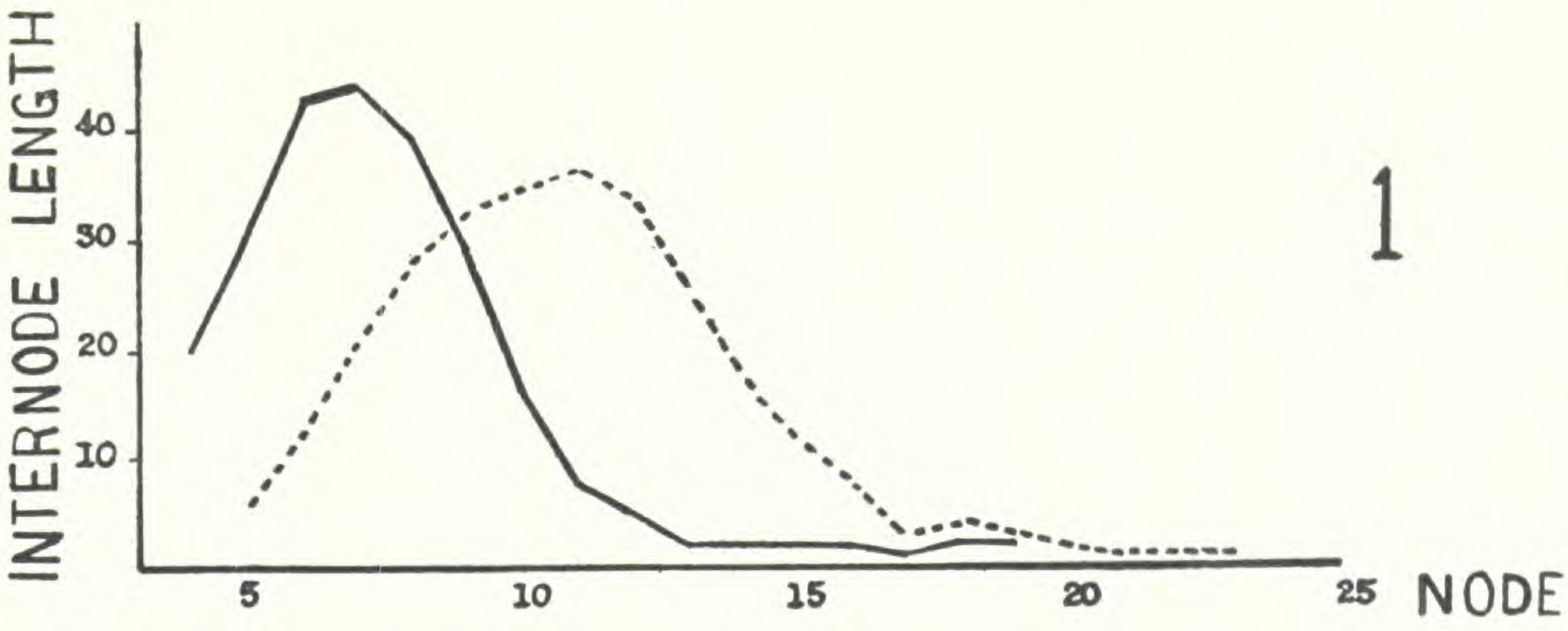
The writer's interest in these problems was first aroused by Dr. Edgar Anderson, who suggested that the disturbances in the normal pattern of development which are found in certain dwarf mutants in maize might be of value in interpreting ear and tassel morphology. A dwarf mutant which occurred as a simple recessive in one of her inbred strains was kindly handed over to the writer for study by Dr. Barbara McClintock. It is the purpose of this paper to report the results of a preliminary comparative study of this mutant and its normal sib, which are believed to have some bearing on the interpretation of tassel and ear morphology.

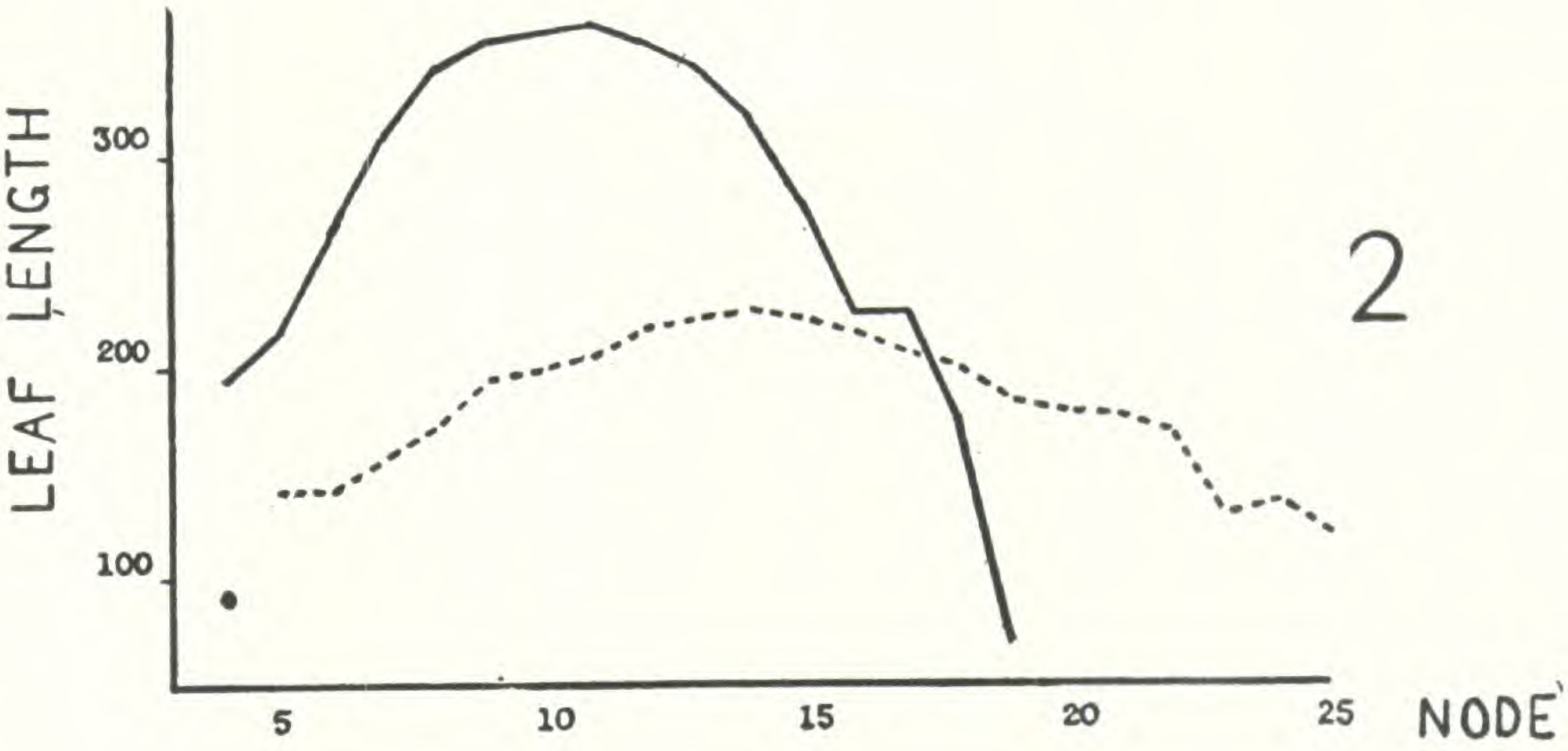
COMPARISON OF THE DEVELOPMENTAL PATTERN IN NORMAL AND DWARF PLANTS

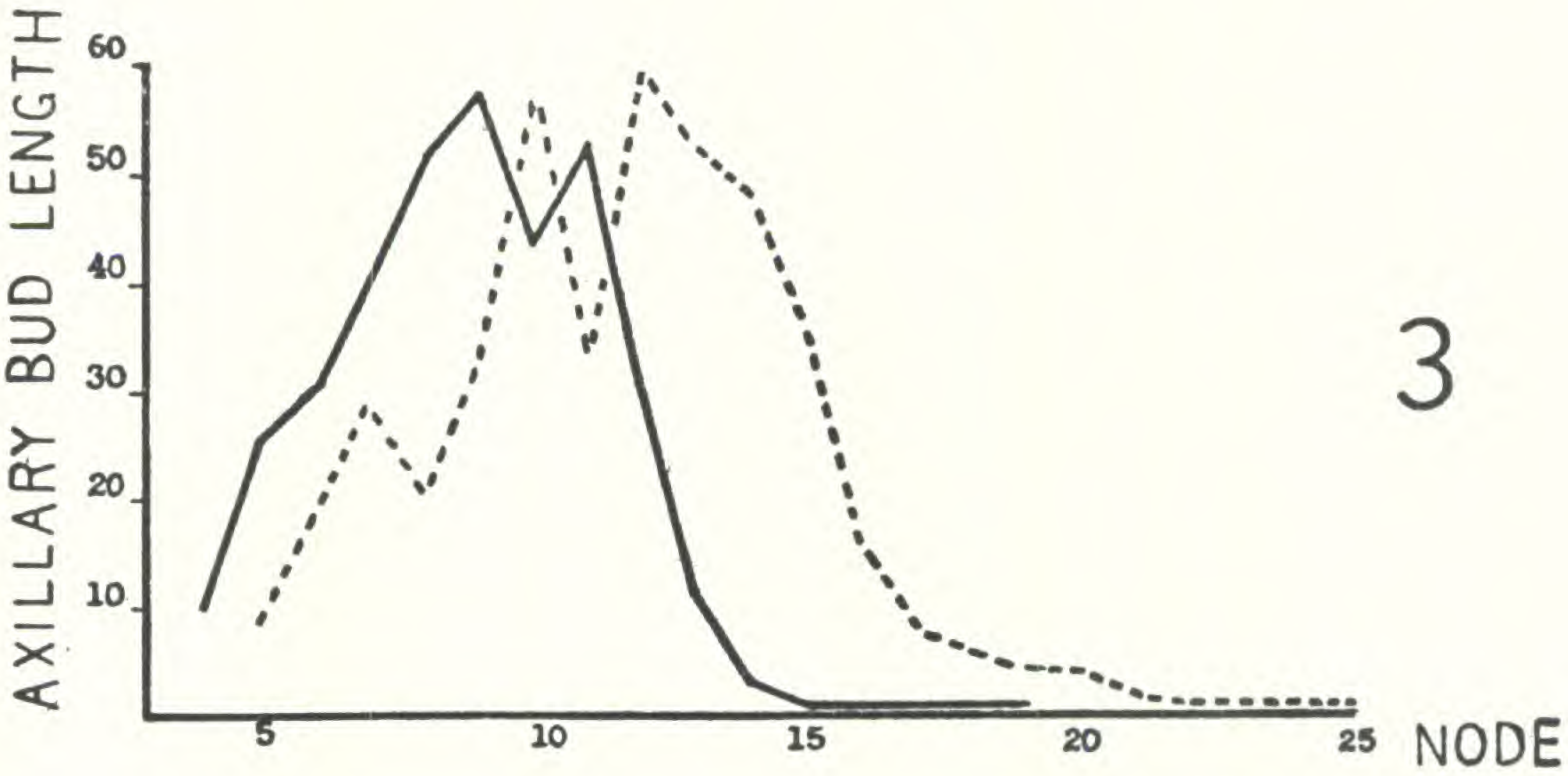
The dwarf mutant segregated out as a simple recessive from a strain, B 97(1). Spontaneous chromosome breakage had occurred in this same strain but the particular line considered in this paper was cytologically normal. In 1945 two plantings of a line heterozygous for the mutant were carried out; the first in March and the second in June. Mutants and normal sibs were therefore available for developmental comparison from the two plantings.

First planting.—It was possible to distinguish mutant plants in the 6–8 leaf stage, as the leaves were shorter and narrower than in normal plants and tended to project at right angles from the main axis. At a later stage the shorter internodes, with the edges of each leaf sheath closely overlapping its neighbor, gave the plant a sort of "cross-gartered" appearance. Tassel emergence occurred at about the same time as in the normal sibs, but owing to the crowded internodes in the mutant, the tassel was never fully exserted above the topmost leaf sheath. Ear shoots were produced later (i.e. at higher nodes) than in the normal sibs, so that the general picture when the silks emerged was a dwarf plant, about half the normal height, with compressed internodes and the upper leaves, ears, and tassel all bunched together at the apex. The clubbed appearance was accentuated by the fact that in no case did the mutant plants tiller, in contrast to the normal sibs which produced 1–3 tillers.

At tassel emergence three normal and three mutant plants were dissected into their component leaves, axillary shoots, and main stem. Measurements of leaf lengths, internode lengths, and lengths of axillary buds were carried out. The first distinguishable node at the base of the stem was considered Node 1, and on this basis average measurements for corresponding parts were determined for normal and mutant plants. A general picture of the course of development during the vegetative phase was obtained by plotting these average values against their corresponding node numbers as shown in figs. 1, 2 and 3. Although the measurements represent averages of only three plants, the curves obtained are relatively smooth and are deemed adequate for illustrative purposes.







Figs. 1–3. Comparative dimensions of normal and mutant plants at time of tassel emergence as shown by internode lengths (fig. 1), leaf lengths (fig. 2), and lengths of axillary buds (fig. 3), associated with successive nodes of the main axis. Normal shown by solid, mutant by broken line.

Examination of the figures shows that in all cases there is a peak in vegetative vigor as measured by size of parts. Internodes, leaves, and axillary buds become progressively larger during the course of development and then decrease in size towards the apex of the shoot. The stage at which the peak occurs is probably associated with the beginning of the reproductive phase, since dissection of young normal plants when 10–12 leaves had been exserted usually showed tassels in the earliest stages of differentiation (c.f. Bonnett, 1940). The largest axillary buds (fig. 3) mark the position of the future ears. In the case of both normal and mutant plants the peak is reached first in internode length, second in length of axillary bud, and third in leaf length. This sequence agrees with Sharman's (1942) detailed studies which showed that during development a "wave of maturation" commences at the tip of each lamina and passes downward through the sheath and internode below. Maximum length should therefore be attained earliest in the lamina and latest in the internode.

Comparison of the data for normal and mutant plants shows that for the three series of measurements shown in the figures, the vegetative peak is reached at a later node in the mutant. At tassel exsertion the mutant has produced more nodes and therefore, also, more axillary buds with subtending leaves. Internodes and leaves are shorter in the mutant than in the normal plant at a corresponding stage, though axillary buds appear to be similar in size. In general, the effect of the mutant gene appears to be a disturbance of the normal pattern of development such that the nodes are differentiated more rapidly, but the growth of associated structures (leaves, axillary buds, internodes) is markedly reduced.

Second planting.—No essential differences from the first planting were noticed during the early stages of growth. As before, mutant plants could easily be distinguished from their normal sibs. At tassel exsertion, however, a striking effect of the late planting conditions was manifested by both mutant and normal plants. In the earlier planted material neither mutants nor normal plants had shown any abnormality in tassel or ear characters. In the mutant, the ears were crowded in the upper leaf axils around the tassel but they were structurally normal. By contrast, at the second planting, while the main axis tassels of "normal" plants were always structurally normal, nearly all the tillers had tassels partially modified towards femaleness. The degree of modification varied considerably; in extreme cases the whole central axis of the tassel was converted into an ear, the laterals remaining staminate, while in milder cases only a few spikelets at the base of the tassel were pistillate. Such partial sex reversal in tillers is not uncommon in certain strains of corn, and is the general rule in others, but the strain under investigation had shown no trace of such a tendency at the earlier planting. It is probable that the environmental factors responsible were either the short day length or cold night temperatures occasioned by the late planting, since both these factors are known to modify the phenotype considerably (Purvis and Gregory, 1937; Went, 1944).

In the case of mutant plants no tillers were produced and dwarfing was more pronounced than at the earlier planting. Dissection showed that the uppermost nodes were extremely crowded, and always telescoped into each other to some extent (pl. 32A). As a result of this crowding the zone of nodes bearing no axillary buds, which normally exists between the uppermost ear-bearing node and the base of the tassel, was almost completely eliminated. Instead, there existed a continuous series of lateral branches, the lowermost members of which were normal ears borne in the leaf axils, and the uppermost members were paired spikelets arising directly on the main axis with no subtending leaf. Between these extremes a continuous graded series could be arranged which is illustrated in plate 32B. The top row from left to right in the plate represents branches borne in the axils of the upper leaves at progressively younger (higher) nodes. The first member of the series does not differ essentially from the normal ears borne at lower nodes, although the ear is very small and the sheathing husks reduced to two. The rest of the series shows a progressive conversion of the ear into a structure indistinguishable from a lateral tassel branch except for a single reduced "husk" at the base. The lower row in the plate shows a continuation of the series, representing lateral branches which occurred above the topmost leaf, i.e. they had no subtending leaf. This continuation of the series shows a graduation from a lateral tassel branch to a paired spikelet borne on the main axis.

Since the effect of the mutant gene at the earlier planting was to crowd the ear-bearing nodes towards the tassel (fig. 3) as compared with the normal plant, its effect at the later planting may be regarded as a more extreme expression of the same process. Here the crowding has been so great that the normally clear-cut sequence—ear-bearing nodes, nodes with no axillary buds, lateral tassel branches—has been condensed so that an intergrading series from ear to lateral tassel branch is the result.

DISCUSSION

The homology of lateral primordia in cereals.—The work of Purvis and Gregory (1937) on the vernalization of winter rye showed that double primordial ridges, occurring at the lower nodes of the main axis in the early stages of development, and the spikelet initials, found at the apex of the shoot, are homologous structures. Towards the base of the shoot the lower ridge in each double primordium develops into a foliage leaf, while at the upper nodes the lower ridge fails to develop and the upper ridge forms a pair of spikelets. The node at which the switch from leaf-forming to spikelet-forming primordium takes place could be varied experimentally by low temperature pre-treatment and also by variation in day length. That this developmental plan is common to all cereals seems likely. Bonnett's developmental studies *(loc. cit.)* of the inflorescences of wheat, barley and oats, showed that at the beginning of differentiation each spikelet is subtended by a lower ridge, which he interpreted as being homologous with the foliage leaves

borne at the lower nodes. In maize he noted that only the female inflorescence showed these subtending ridges. Certain species of barley regularly have their lower spikelets enclosed by large leaf-like structures, clearly homologous with the leaves borne at lower nodes. Occasionally, too, in oats an aberrant plant occurs in which a structure indistinguishable from a lateral panicle branch is borne in the axil of the topmost leaf sheath. Sharman (1942) concluded that the subtending leaf and the axillary bud occurring at each node of the shoot are botanically unrelated structures, the former being anatomically associated with the internode below, and the latter with the internode above. However, whether it is more correct to think of double primordia, or two distinct initials which are always borne in juxtaposition, does not affect the main issue—the homology of tassel branches and axillary buds (ear-shoots). The mutant described in this paper, which exhibits a continuous range of expression from axillary ear shoot to lateral tassel branch, provides developmental evidence of the correctness of the anatomical theory.

Since tassel branches and axillary buds (ear shoots) are homologous, they must represent different stages in a developmental series and it might be expected that the developmental processes which have operated in forming the tassel would leave traces in axillary buds, i.e. in ear shoots and tillers. This expectation is supported by Anderson's discovery (1944) that degree of condensation of the lateral tassel branches is strongly correlated with the number of rows in the ear. It would seem that where an unbroken series of primordia can be induced to develop, as in the mutant described here, it should be possible to distinguish acropetal gradients in the processes affecting the development of the inflorescence. These may be considered in relation to the three questions suggested in the introduction of this paper.

Reduction of lateral branches.—Reference to pl. 32B shows that in passing from lower to upper nodes, i.e. from ear-bearing nodes to nodes bearing paired male spikelets, there is a gradual decrease in the number of parts borne by the axillary branches. This begins as a reduction in the number and size of the husks enclosing the lateral branch (see top row) and continues as a reduction in the number of spikelets (see bottom row). In the normal maize plant this progressive series is broken, because the intermediate stages are suppressed (there is a zone of nodes between the topmost ear-bearing node and the node bearing the lowermost tassel branch, which carries no axillary buds). The disturbance in normal development exhibited by the dwarf mutant eliminates the sterile zone and in doing so clearly demonstrates that reduction in spikelet number in passing from base to tip of the main axis of the tassel is but a continuation of a process initiated earlier in the vegetative parts of the plant.

Condensation of nodes.—Condensed nodes were frequently found in the main axis of mutant plants, an example of which is illustrated in pl. 32A. In this illustration the number of leaves borne at each "node" or condensed group of nodes is

indicated by the white figures. The lowest "node" shown in the illustration carried two leaves and it can be seen that the "node" really consists of two adjacent nodes with a very short internode between. The next "node" bore six leaves, which suggested that it consisted of a complex of at least six nodes, though only two nodes joined by a spiral ridge are visible externally. The four higher "nodes" bore no leaves and appear to be simple, but the fact that they bore three, five, and five lateral branches respectively, throws doubt on their apparently simple structure and suggests rather that each "node" is in reality a complex of several nodes.

Other evidence of condensation is illustrated in pl. 33. The leftmost picture (a) shows a portion of a tiller of a normal plant which bore a tassel partly modified towards femaleness (tassel-ear). Examination of many such tassel-ears showed evidence of node condensation. Next in order from left to right (b) in pl. 33 is a portion of an axillary branch which developed at a node below the usual ear-bearing region in a normal plant. This branch was induced to develop by extirpating the main axis tassel at an early stage of development. Although a normal ear was borne by this branch, the shank is greatly elongated and structurally similar to a tassel-bearing tiller, but shows condensation of nodes. The two rightmost illustrations (c) and (d) from normal plants show ears borne on long shanks which again show node condensation. In the case of all four branches illustrated in the plate, the nodes below the condensed region bore only one leaf per node, but above the condensed region, more leaves than visible nodes were always present. *This condition would seem to be true for normal ear-bearing branches in general, since careful examination shows that the number of husks enclosing the ear is always greater than the number of distinct ridges on which they are borne.*

It seems to the writer that the association of the ear structure with a region of condensed shank nodes immediately below it may be of developmental significance. Examination of many condensed regions similar to those illustrated in pl. 33 suggests that condensation begins with a twisting of the axis. If the twisting is severe, the node becomes tilted to one side and fused with the node immediately below. In other words, the series of separate ridges becomes converted into a continuous helical ridge. Further twisting results in a suppression of the internode between the gyres and a consequent fusion of neighboring gyres. When neighboring gyres are fused a multiplication of axillary structures (leaves and axillary buds) results. The stages leading to this multiplication can only be recognized in suitable material like that illustrated in pl. 33, but it may be suggested that an acceleration of the same process underlies the multiplication of spikelets in both ear and main axis of the tassel. If this interpretation is correct, the "nodes" of the male and female inflorescences which exhibit a polystichous arrangement of spikelets represent complexes of nodes, each sub-unit of which bears two spikelets. The condensation initiated in the shank would be continued and intensified in the ear itself. The normal tassel, since no leaves subtend the lateral branches, provides no

clue as to its complex nature, but the same underlying structure seems evident from the condensation exhibited by the abnormal mutant tassel illustrated in pl. 32A. Furthermore, this interpretation appears to be the simplest way of explaining the correlation between degree of tassel condensation and ear row number which has been demonstrated by Anderson (1944).

It might be argued that the chance fusion of nodes with accompanying multiplication of parts could only produce an irregular arrangement of spikelets in the inflorescence, whereas the row number found in the ear is a very regular and constant feature. This, however, would ignore the obvious, though little understood, laws of organized development which underlie phyllotaxy. The mechanical precision with which repeated structures are arranged in relation to one another has been stressed by Thompson (1942). He has shown that diverse problems of phyllotaxy may be interpreted, though not explained, in terms of rather simple mathematical constants. Thus the position of an axillary bud, pair of spikelets or leaf, appears to pre-determine or (in the mathematical sense) generate the position of the corresponding structure at the succeeding node. In a perfect alternate distichous arrangement, one structure generates the position of the next at an angle of 180° in respect to the main axis. If the angle is a little more or a little less than 180° a helical twist is superimposed on the distichous arrangement, as can often be seen in the arrangement of leaves on a young maize plant. Now, if two nodes become fused, it would appear that each pair of spikelets would act as independent generators in the production of spikelet pairs at the succeeding node, and this process might be expected to continue in an orderly fashion without further fusion of nodes. In short, a 16-row ear does not require a repeated fusion of nodes in groups of eight, but merely that eight nodes shall be condensed *once,* and that the eight spikelet pairs shall each generate a spikelet pair at successive nodes. Since an apparent fusion of six nodes can be seen in the abnormal tassel shown in pl. 32A, fusion of this order would not appear to make undue demands on the anatomical structure of the axis. It may be noted that the mechanisms suggested would be applicable to panicles in general, and not confined to the maize inflorescence.

If condensation of nodes is the explanation of the change from a distichous to a polystichous condition, there would appear to be a gradient of increasing condensation from the base to the apex of the main axis, and from the base to the apex of all axillary branches, i.e. in the tassel from the lower distichous lateral branches to the upper polystichous central axis; in the ear shoot from the lower nodes in the shank bearing distichous sheathing husks to the upper spikelet bearing nodes which are all polystichous. Normally, condensation is synchronized rather closely with the switch from vegetative primordium to spikelet initial, but when the synchronization is disturbed, either by environmental effects or by mutation which modifies the normal growth processes, as in the mutant described here, the mechanism of condensation can be observed in the vegetative phase of development.

The determination of maleness and femaleness.—The material considered in this paper sheds little light on the mechanism which determines whether male or female spikelets shall be produced. Within the restricted limits of the material examined, however, the following generalizations appear to be valid:

(1) An axillary branch bearing an inflorescence which exhibits a greater or less degree of femaleness is usually associated with obvious condensation in its lower, leaf-bearing nodes.

(2) In inflorescences of mixed sex, it is the more condensed nodes which tend to bear female spikelets. Thus it is usual for the central condensed axis of a tassel-ear to bear female spikelets; the lateral, less condensed tassel branches are preponderantly male.

(3) Tillers (i.e. axillary branches which develop independent root systems) bear tassels or tassel-ears. Axillary branches, when induced to develop by tassel extirpation at nodes *below* the normal ear-bearing nodes and *above* the tillers, usually bear ear-shoots.

(4) The inflorescence borne at the apex of the main axis and the inflorescence borne at the apex of a tiller are labile in respect to sex; the switch mechanism being affected by day length and/or thermoperiodicity.

SUMMARY

(1) A comparative developmental analysis of a recessive dwarf mutant with its normal sib in maize suggests that the dwarfing gene: (a) increases the production of nodes and associated axillary structures; (b) reduces the lengths of the internodes, leaves and leaf sheaths; (c) delays the production of axillary ears so that the sterile zone, normally existing between the uppermost ear-bearing nodes and the lowest tassel branches, tends to be eliminated.

(2) Under suitable conditions the axillary branches in the dwarf mutant exhibit a graded series, ranging from normal ear to paired male spikelets.

(3) Within this graded series the following tendencies are evident:

(a) Progressive reduction in number and size of the lateral organs borne by the axillary branches in passing from base to apex of the main axis.

(b) Progressive condensation of nodes from base to apex both in the tassel and in ear-bearing axillary branch (shank).

(c) Association between degree of condensation and femaleness.

(4) The observed tendencies are used to suggest a probable interpretation of the morphology of tassel and ear in the normal maize plant.

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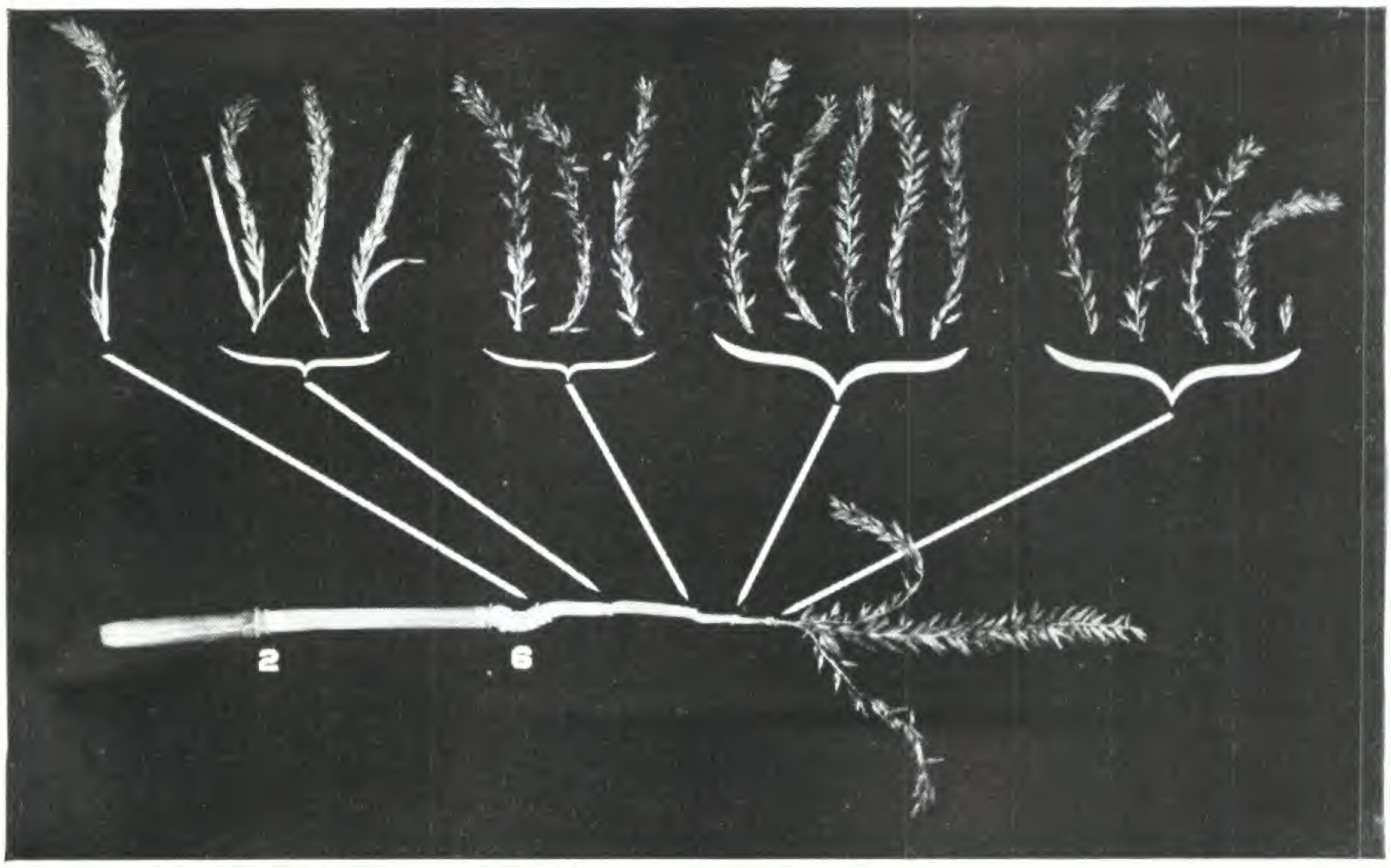
Explanation of Plate

PLATE 32

Fig. A. A dissected tassel and uppermost nodes of the main axis in a late-planted mutant. Figures indicate the number of leaves removed from each node; the position of the lateral branches is indicated by lines.

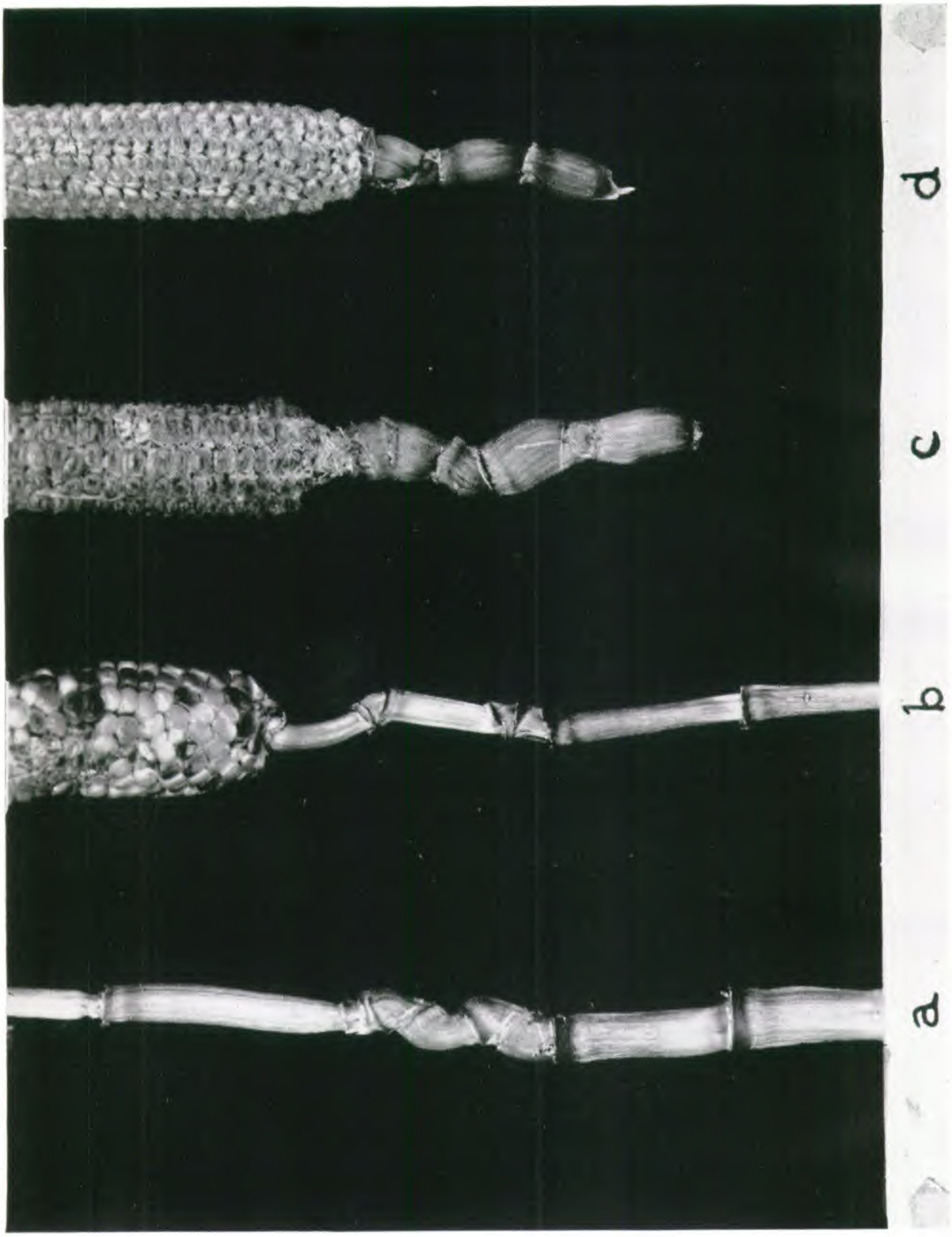
Fig. B. A range of lateral branches occurring in late-planted mutants, in a region corresponding to the sterile zone of the main axis in a normal plant. Upper row—lateral branches borne in the axils of foliage leaves; lower row—lateral tassel branches arising at nodes with no subtending leaves.



A

B

STEPHENS—TASSEL AND EAR OF DWARF MUTANT



STEPHENS—TASSEL AND EAR OF DWARF MUTANT

Explanation of Plate

PLATE 33

Evidence of node condensation in "normal" plants. From left to right (a) main axis of a tassel-ear, (b) female axillary branch induced to develop by tassel extirpation below usual ear-bearing nodes, (c) and (d) axillary branches bearing normal ears on abnormally long shanks. In all cases at nodes below the condensed region leaves were borne singly, while nodes above the condensed region bore two or more leaves each.

STUDIES ON THE STRUCTURE OF THE MAIZE PLANT

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There is a basic pattern for most grasses and this pattern is repeated throughout each plant, in reproductive as well as vegetative parts. The main axis of the maize plant bears leaves and buds on opposite sides of successive nodes. This pattern extends to the branches, the tassel, and to the ear. In the maize tassel and ear the parts and even their arrangement may be modified, but the basic arrangement is still that of the stem of any grass. This can be seen easily in the lateral branches of the tassel and in ears with only four rows of grain.

All parts of the maize plant are made up of similar units. The name "phytomer" has been applied to these (see Esau, 1943, for a discussion of this as applied to the stem). A phytomer consists of an axillary bud at its lower end, a section of the stem (the internode), and is terminated by a leaf. It corresponds to Collins' (1919) *alicole*, although his original definition included only the spikelet or pair of spikelets and not the associated portion of cob or stem.

Because the maize pattern is repeated throughout the plant we can expect almost any change in one part to be repeated in homologous parts. For example, when hairs on the leaf sheath are large and numerous, there will be large and numerous hairs on the glumes of tassel and ear. Because of this repetition of plant pattern, some organs which are not strictly homologues will reflect changes in other parts. Thus, in one race of Bolivian maize, when the tassel branches and the rows of spikelets on the central spike are nearly doubled in number, the number of rows of grains on the ear and vascular strands in the stem are correspondingly increased.

The extent of variation in the grasses is greatest in the flowering parts and least in the vegetative areas of the plant. Thus the leaves are still arranged dichotomously in the Bolivian maize even though the number of tassel branches and rows of grains has been doubled.

MATERIALS

Maize.—

We studied most of the known varieties of maize in our plantings in Brazil, Bolivia, Cuba, and the United States. Some others we were able to study in the field or in dried specimens of ears. Plant-breeders and geneticists furnished material of especially interesting mutants. Two collections of this material were of great interest. One was the Central American and Mexican maize assembled by Dr. Paul C. Mangelsdorf and from which many chromosome knob positions had been determined by Dr. James Cameron. The other was a collection of inbred lines for which Dr. William L. Brown had mapped chromosome knob positions.

Teosinte.—

Some teosinte was collected in Guatemala but most of the studies were based on material grown from seed in Bolivia. For convenience we use the common name, teosinte, instead of the combination *Zea mexicana* (Shrad.) Reeves & Mangelsdorf.

Tripsacum.—

Most of the studies were made on *Tripsacum australe* Cutler & Anderson, not only because this was the one on hand when the work was under way in Brazil but because it has been reported to lack terminal knobs on the chromosomes (Graner & Addison, 1944), and is the most southern of the 18 (n)-chromosome *Tripsacum* species.

Manisuris cylindrica (Michx.) Kuntze.—

Material of this species was collected in Texas and Florida. A series of related varieties was studied in herbarium material from southeastern United States.

METHODS

Most of the studies were made on dried ears and tassels. The cobs and glumes of many varieties, especially some from North and Central America, were hard to dissect so young green ears grown in Brazil, Bolivia, Cuba, and the United States were used for these varieties. Young ears have nearly all the characters of a mature ear except color.

In cases where paraffin sections were desired, ears collected the day the silk appeared were fixed in Carnoy's fixative. At this stage most of the structures are fairly well formed, although their relative sizes are not the same as those in the mature ear. After being embedded in paraffin these ears could be cut easily and safranin- and haematoxylin-stained sections studied and compared.

Many cross- and longitudinal-sections of the stem and ears were cut free-hand and photographed by floating them onto a glass plate in the negative holder of an enlarger. The projections of these sections, made on standard enlarging paper, were studied, compared, and measured more accurately and rapidly than would be possible with the sections themselves.

When the retting methods described by Evans (1928), Sharman (1942), Reeves (1946), and Laubengayer (1946) are applied carefully, good preparations with a clearly visible network of vascular strands are obtained. We immersed some bundles in a vial of stain as directed by Evans (1928), but, since we wanted to follow more strands and had only a limited number of plants, it was more convenient to inject the stain with glass tubes which were drawn out to hypodermic needle-like points. With these we could inject several colors and trace their separate courses in the same plant. By filling the tubes one-quarter full of tap water while they were being inserted, staining of the outer rows of bundles

was avoided. Stain was added after the tube was fastened to the stem, tassel, or ear with Scotch tape. Aqueous solutions of eosin, methyl blue, and Bismarck brown were used. The tubes usually were left in place for two days although stain was carried through several nodes in a few hours.

ARRANGEMENT OF THE PHYTOMERS

If one considers the maize plant to be made of units which are moved into place like bricks in a house, then it is necessary to consider the plant as based on a spiral arrangement with each unit rotated 180 degrees. This makes the polystichous structure of the ear and the central spike of the tassel dependent only upon a change in the pattern of phyllotaxy (Weatherwax, 1935), a change which can be seen in other plants (Brieger, 1945). There have been attempts to trace this pattern in the ear and tassel. The method which shows greatest promise has been used by Mangelsdorf (1945) and takes advantage of the fact that in the distichous lateral branches of the maize tassel, and in the staminate inflorescences of teosinte and *Tripsacum,* the two rows of paired spikelets are arranged so that the pedicellate spikelet of one pair is adjacent to the similar spikelet of the other. Thus as one goes around a staminate branch of maize, teosinte, or *Tripsacum,* the spikelets are sessile, pedicellate, pedicellate, sessile. The main difficulty in applying this method is that the vertical distance between paired spikelets of the tassel is not always the same and it is necessary to measure carefully. In the ear, on the other hand, this distance is quite constant, and notations of the sessile and pedicellate spikelets can be made on squared paper. With many ears it is difficult to distinguish between pedicellate and sessile spikelets and on some ears practically impossible (Cutler, 1946). Where we have been able to apply this method to the ears, our results agree substantially with those of Mangelsdorf. There is a strong tendency to a longitudinal arrangement, a tendency made conspicuous by the vertical course of conductive tissue.

The major vascular strands run longitudinally, and although there are some connections at the nodes these are so weak that very little stain is carried to other rows of phytomers. The weakness of these connections may be seen in some maize ears with a large cob. Most of these will split longitudinally between rows of paired spikelets but resist breaking between the paired spikelets of a row, and to a lesser extent, across the rows of paired spikelets.

As an aid to the study of the relationship of the parts of the plant, we found it convenient to study the course of the vascular system. The plant may be considered to be made up of leaves, the stem to be composed of leaf traces. In the upper parts of the tassel, the number of vascular strands in the main axis is very small, and the number increases as we descend the stem and the traces of more leaves enter. Plants with many tassel branches, many nodes, and many rows on the ear usually have many vascular bundles. The number of vascular bundles in an ear appears to be larger in those ears with more grains in a longitudinal row.

An apparent contradiction to this is found in the position of ears on a single plant. Usually the highest ear has the largest number of rows of grains, and those ears borne lower on the stem, although there are more vascular bundles in the stem at the node from which these ears originate, have smaller numbers of rows of grains. In lines studied by Burdick (1947), the uppermost ears usually had eight rows of grains while the lower ears usually had four rows. Burdick attributes this to the differentiation and development of the lower ears under less favorable physiological conditions. In our observations on a large number of varieties with a wider range of row numbers, we have found Burdick's observations to be valid. Exceptions are found when a large number of ears are borne on one plant as happened on one of our crosses of Bolivian highland maize with Golden Bantam. The ear borne at the sixth node had twelve rows of grain; those at the fifth and seventh nodes had ten; at the fourth, ten; at the third and eighth nodes, eight rows. An undeveloped ear at the second node had eight rows. With the exception of plants with eight-rowed ears our notes on South American maize plantings show that the number of rows of grain on two ears from the same plant is rarely ever the same. Our notes also show that in most varieties, and again we except those which bear ears with eight rows of grains, the number of rows on the ears is greater on plants with a higher number of nodes and a higher number of vascular bundles.

There are two groups of vascular strands, the peripheral and the central or medullary. The strands pursue a nearly vertical course and these systems tend to remain distinct. When the traces from a leaf or homologous structure enter the main axis, most larger and more median bundles go almost immediately to the central region while the smaller bundles remain in the periphery and after a few nodes unite with some of the other peripheral bundles or progress to the center. The two systems are present in stem, tassel, and ear of maize, and in homologous parts of teosinte, *Tripsacum*, and *Manisuris*. The vascular system of the maize stem has been studied by Hershey and Martin (1930), Esau (1943), and Kumazawa (1940); that of the tassel by Kumazawa (1939, 1940a), and that of the ear by Reeves (1945, 1946), and by Laubengayer (1946). While there have been some studies on the relation of the stem structure to stiffness of stalk (Magee, 1948), none of the investigators has worked with a wide variety of material. There is an opportunity here for investigations of considerable practical value especially now that mechanical corn pickers are used and lodged corn stalks are more of a nuisance.

AXIS, STEM, RACHIS, COB

The axis is usually somewhat cylindrical in the stem and other distichous parts, but in a polystichous axis, like that of a many-rowed ear, the axis of each phytomer is a pie-shaped segment. Usually there is a hollow above the bud or branch. In the stem and tassel this is a longitudinal groove and in the ear a pit

or alveole. The alveole is very pronounced in teosinte, *Tripsacum*, and *Manisuris*, and its margins may partially enclose the spikelet. In some South American races of maize like "Coroico" (Cutler, 1946) and some varieties from the highlands of Peru and Bolivia and parts of Chile and Ecuador these margins or rachis flaps are inconspicuous. In other varieties, especially some of Mexico and southwestern United States, they are prominent.

For a long time we thought that prominent rachis flaps were always associated with *Tripsacum*-contaminated maize and with a high number of knobs on the chromosomes. Using chromosome knob positions determined by Dr. James Cameron for a large number of Guatemalan and South American samples of maize, and positions determined by Dr. William L. Brown for a selection of common commercial inbreds, we tried to find some correlation between the presence or absence of certain knobs and variations in the structure of the maize spikelets, both male and female. In some of the Guatemalan material there appeared to be a good correlation between prominent rachis flaps and the presence of a knob on the long arm of chromosome 3. Examination of more material showed us that not only was this incorrect, but that rachis flaps are not always correlated with high knob numbers. Some of the North American inbreds with only one chromosome knob have more prominent rachis flaps than others with seven or eight knobs.

The rachis flap resembles the auricle of the leaf in shape and this resemblance is heightened by the presence below it of the pulvinous notch, a small notch often formed at the margins of a leaf, bract, or glume, at the point of its union with the node. Like an auricle notch, it usually bears numerous hairs.

The sulci, or grooves between rows of alicoles or phytomers of the maize ear, are often deeply cut into the cob. We have found no definite geographical distribution of sulci, but they are most prominent in many-rowed ears from the Andes, Mexico, and our Southwest. In some races, as Coroico, and Altiplano from the Bolivian highlands, sulci are rarely ever present.

The vascular strands supplying the paired spikelets of the maize ear may separate nearly at once after branching out from the longitudinal vascular system but often may remain together for several millimeters. The latter is the case in some South American maize and in these varieties the paired spikelets are usually raised above the alveole. In marked contrast to this are spikelets attached so closely to the cob that they are turned toward the tip of the ear and do not lie perpendicular to the longitudinal axis of the cob.

The rachilla on which the spikelets are borne is surrounded in part by the glume. About the base of the rachilla of each spikelet of the ear is a small callus. One of the pair of spikelets is usually borne lower on the glume than the other and is surrounded by a small ring of unicellular hairs. This lower spikelet appears to correspond to the sessile one of the tassel. The rachilla of the maize spikelets is variable in thickness and in the length of its internodes. In some *Tripsacum*

and in *Manisuris* the rachilla is quite slender and the glumes, lemmas, paleas, and other parts are well separated. In teosinte and other species of *Tripsacum*, notably *T. dactyloides*, the rachilla is compacted and the parts close together. The grains of corn ears which have glumes raised above the ear and have longer and/or more slender rachillas can be pushed into the ear. The sessile ones with a compacted and short rachilla are firm. In most Guatemalan maize Andean varieties (Mangelsdorf & Cameron, 1942) could be distinguished from tripsacoid varieties by the ease with which the first could be pushed in. Ease of shattering is related not alone to the longer rachilla but to the weaker attachment of the grain to the rachilla. In segregates from crosses of Golden Bantam and Country Gentleman sweet corn many of the grains fell readily from the ear even though they were borne on compacted rachillas. This is a desirable characteristic in corn to be eaten on the cob, for the grains can be removed without the annoyance of particles of glumes and pericarp catching between the teeth. After the grain has been eaten the cob is clean and neat.

THE NUMBER OF SPIKELETS

Many of the Rottboelliae, the tribe of the Andropogoneae to which *Zea* and *Tripsacum* should belong and to which *Manisuris* does, have only one spikelet in each phytomer. In this spikelet are usually two flowers. The upper one is usually perfect and bears both pistil and stamens; the lower one is usually staminate and does not produce seeds. In cases where two spikelets are produced, one is often non-functional or staminate, while the other bears stamens and pistils. In the tassels of maize which bear seed, the sessile spikelets usually bear the seeds while the pedicellate ones remain only staminate. In teosinte and *Tripsacum* the staminate portions of the inflorescence have a pair of spikelets in each alveole, but the pistillate portion usually has only one which is functional, although a second one may occasionally develop into a functional staminate spikelet or even into a functional pistillate spikelet. Occasional clones of *Tripsacum australe* have numerous pistillate alveoles which bear pairs of spikelets. A complete series of the possible combinations in a pair of spikelets can be found in *Tripsacum*, teosinte, *Manisuris*, and maize. They are common in segregates from teosinte-maize crosses. Both spikelets may be staminate or both pistillate. When one is pistillate the other can be a pedicelled or non-functional staminate spikelet or a pedicellate and non-functional pistillate spikelet.

In maize there is nearly always a pair of functional pistillate spikelets. An exception to this was discovered by Langham (1940) in an inbred line of maize while he was making a study of single *vs.* paired pistillate spikelets in teosinte and teosinte-maize crosses. Langham concluded that the single pistillate spikelet of teosinte is governed by a single gene recessive to paired spikelets. Although he makes no mention of the tassels of his plants with single spikelets in the ear, it is probable that the tassels were not influenced by the gene he found, for Langham

was studying other tassel characters and would most likely have noticed any differences. Besides, if it is the same gene as that in teosinte, it is unlikely to have any effect on the tassel because the tassel of teosinte has paired spikelets even though these are single on the pistillate inflorescence.

Hepperly (1948) discovered an ear with single spikelets in an inbred line of corn belt dent, and has been studying this character. Hepperly told us that the tassels of his plants were different and those of the plants we have grown from seeds he supplied usually have the pedicellate spikelet of the pair reduced and nonfunctional but still present. There is a series of degrees of reduction of the one spikelet of the tassel, and it would be interesting to transfer Hepperly's single spikelet character to different races of maize and study any modifier complex which might be present.

Maize plants bearing teopod or corn grass genes are extremely variable in habit and in composition of inflorescences. Frequently in corn grass, and occasionally in teopod, many of the pistillate alveoles will have only one spikelet although both flowers of this may function and the spikelet will have two grains.

Illinois R4 is a corn-belt inbred line used in many combinations for the production of hybrid corn seed, but its rows of grains are usually so irregular that it is used only as the pollen parent. On many ears it is difficult to distinguish definite rows. The tassel is also more irregular than most. In R4 only one spikelet bears grains in some of the alveoles, although the other spikelet is present. The distribution of the alveoles with only one grain is occasionally so regular that the ear has an odd number of straight rows of grain over part of the ear. In spite of this we have been unable to distinguish any constant pattern for the distribution of the undeveloped spikelets.

Extra spikelets in an alveole are common in maize and are occasionally found in *Tripsacum* and *Manisuris.* Often the maize tassel will appear to bear several additional spikelets in each alveole which upon close examination may prove to be two nodes close together. This is caused by condensation of an internode (Anderson, 1944) and is distinct from multiplication (Cutler, 1946) by which additional spikelets are formed by branching within one alicole. Multiplication of spikelets within one alicole is common in the basal rows of many varieties of ears. It produces enlarged butts with irregular rows of grains. The additional spikelets are added in the same plane as the two usual ones and are forced out of line by the surrounding grains.

There are some cases of multiplication of number of spikelets in each alveole of the ear in which the additional spikelets are not borne in the same plane as the two usual spikelets but appear higher up on the ear in the same alicole. The first ears we found were among some of Dr. F. G. Brieger's crosses of pod corn with Chavantes Indian corn. These had four pairs of spikelets in some alveoles, two of them with their first glumes facing the butt and two others with their first glumes towards the tip of the ear (Cutler, 1945). The embryo of the upper grain

in the extra spikelet faced the butt just as would one which would develop in the lower flower of the usual spikelet. The extra spikelets were also found in the tassel.

Another ear with additional reversed spikelets was found in some of Dr. Mangelsdorf's collections. In this case only one spikelet was added to the usual pair but the extra one was reversed just as in Dr. Brieger's material, and the grain, even though produced from the upper flower, had the embryo on the side towards the butt. None of the alicoles on Dr. Mangelsdorf's ear had more than three spikelets and most had the usual two. We do not have a tassel from the same plant and ears grown from this seed did not have the extra spikelets.

Most studies on the structure of the ear substantiate the theory that the ear has arisen by the suppression of branches of an inflorescence. It is not surprising, then, that we occasionally find ears with more than two spikelets in each alicole. There are extremes in which the ear branches freely and looks like a greatly thickened tassel. So numerous and crowded are the branches of the tassel and ear that the plants in some variations do not produce seed. The structure of the inflorescence produced in a plant bearing the gene *ramosa*, a gene which controls one of the extreme branching types, has been described by Kempton (1921).

In most experimental fields one can find examples of flowering branches produced in the ear because they are especially common when the plant is disturbed by the presence of genes like teopod, tunicate and some of the tassel seed genes, which have radical effects, or by unnatural growing conditions, especially a change from the usual length of day to which the plant is adapted.

FLOWERS

Usually a spikelet has two glumes enclosing two flowers. The normal flower of maize, teosinte, *Tripsacum* and *Manisuris* consists of a lemma, a palea, two lodicules, three stamens, and a tricarpellate single-seeded ovary with two stigmas. In some flowers the ovary is undeveloped and in others the stamens do not develop. Functional stamens and ovary occasionally develop in the same flower, and are the rule in the upper flower of the *Manisuris* fertile spikelet.

In the Andropogoneae the upper flower usually is perfect while the lower one does not produce seeds but often bears stamens (fig. 1f). Exceptions to this are common in maize, and in one variety of sweet corn, Country Gentleman (fig. 1c), most spikelets bear two grains. The spikelets of teosinte and *Tripsacum* and *Sorghum* frequently have two grains but we have not seen this in *Manisuris*.

Even though Country Gentleman corn has been grown in many parts of the United States, two-grained spikelets are rare in other varieties of corn in North America. In South America there is no variety of maize which is characterized by two-grained spikelets, but a few spikelets with the lower flower developed are found in occasional ears of almost all varieties of highland maize.

The embryos of grains which develop in the upper flower face the tip of the ear while those which develop in the lower flower face the butt. Not all grains with their embryos on the lower side are produced in the lower flower,

and two exceptions, cases in which the alveoles had more than the usual pair of spikelets, have been mentioned. Another exception is to be found in the tips of ears of northern flint and flour corn. On a few ears we have found occasional twisted spikelets with the grains turned so the embryo faced to one side or even to the butt of the ear.

The lower flower develops later than the upper, and the grain must push into any space left between the earlier-appearing grains. Usually all the grains are so pushed out of line by this that there is no semblance of regular rows. Occasionally, however, the later lower grains are forced out to the side of the upper grains of the paired spikelets and become arranged in a straight row of small grains beside the ones from the upper flower.

The later maturation of the lower flower makes it difficult to see which ears bear the double-grained spikelet character when ears are hand-pollinated early in the season. All the fertilized grains may, if the lower ones have not yet developed silks, be borne in the upper flowers. When the ears are pollinated after the silks of the upper flowers are no longer receptive, grains are produced only in the lower flowers.

In some of Dr. Brieger's Brazilian popcorn we found ears with grains in both flowers but with the lower grain poorly developed and lacking endosperm. In appearance the extra grains resembled the structures described by Weatherwax (1925) as originating in the positions of the flower usually occupied by the stamens. These defective grains in the Brazilian popcorn did not develop in most cases unless the upper grain developed. The absence of embryo and endosperm in most of them suggested that they developed parthenocarpically but needed the stimulation of the normal grain in the same spikelet.

In our plantings of two-grained spikelet varieties in Bolivia, the character appeared to be controlled by a single recessive gene acted upon by several modifiers. In their study on Country Gentleman sweet corn, Huelsen and Gillis (1929) suggested that the two-grained spikelet character was controlled by two recessive genes. Since their classification was based on irregular *vs.* straight rows, it is possible that some ears which had a few of the lower flowers developed escaped notice because only one of the flowers in the spikelet was fertilized. A better way to classify ears for this character is to search for grains with the embryo on the butt side. It is possible that Country Gentleman corn and many of the two-grained spikelet ears from South America may bear an identical single recessive gene controlling development of the lower flowers.

There are several known genes which affect the development of the lower flower. Plants with the tunicate gene often have grains in the lower flower, sometimes even in the tassel. In plants bearing the gene for teopod, for any of the several for tassel seed, for silky, and for the "corn grass" which Dr. Singleton is studying, the lower flower usually develops.

Occasionally the stamens,, as well as the ovary, develop in the upper flower, or even in both upper and lower flowers on the ear. More commonly the tip of the ear bears purely staminate spikelets which are similar to those of the tassel.

Sometimes more than two flowers are found in the spikelets. Weatherwax (1925) has described cases in which several flowers, both pistillate and staminate, were found.

LEAVES, BRACTS, GLUMES, LEMMAS, PALEAS

That the ear of maize, and the central spike of the tassel, too, originated from the suppression of lateral branches is further suggested by the frequent occurrence of small ears in the axils of many of the husks below the main ear. Although husks or bracts are not usually found in the corn ear or tassel, one or two of the lower pairs of spikelets on an ear will occasionally be subtended by them, and the branches of the *ramosa* inflorescence mentioned earlier are often subtended by bracts. Bracts are commonly found subtending the spikelets of two peculiar mutants, teopod and corn grass.

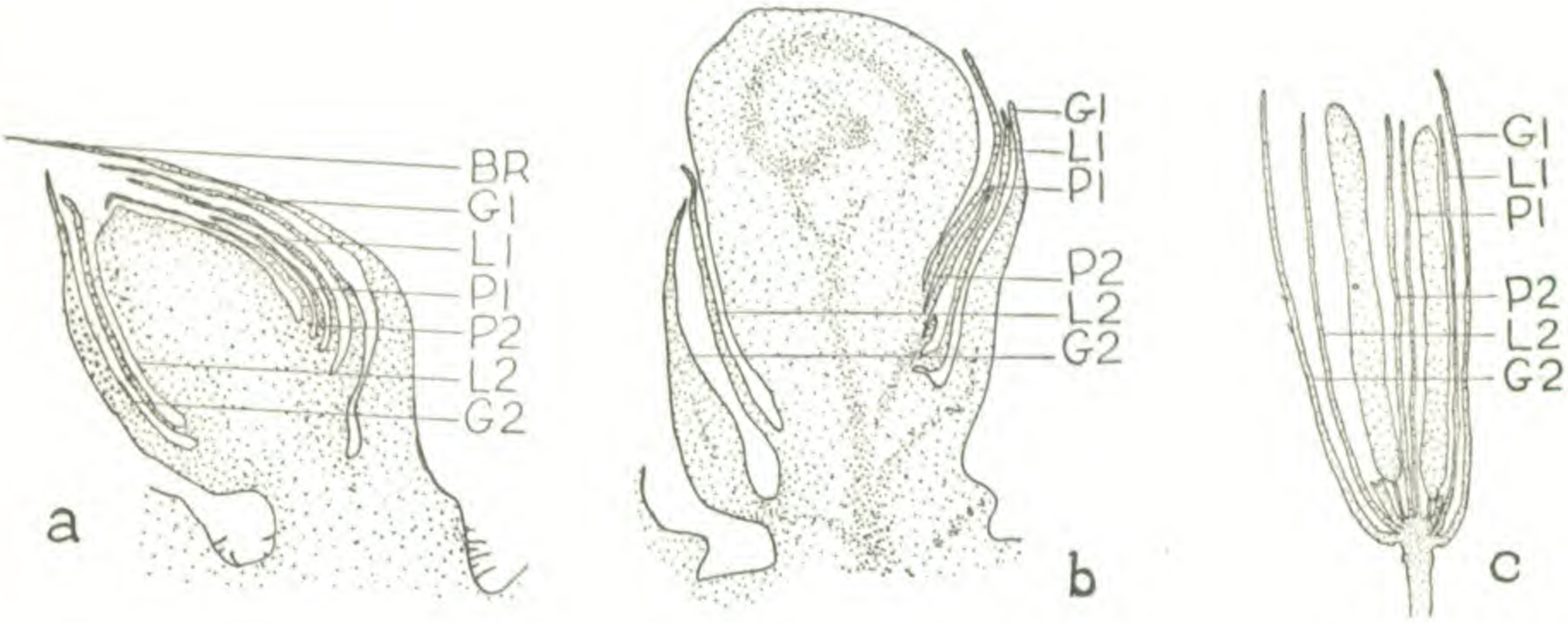

Fig. 1. Median longitudinal sections through a single spikelet of (a) teopod maize ear, (b) normal ear, (c) maize tassel.

Teopod is a dominant mutant gene on chromosome 7 which was described by Lindstrom (1925) and has been studied morphologically by Weatherwax (1929). Plants bearing this gene are extremely variable and many forms resemble teosinte in habit. On most of the plants, each pair of spikelets, in both tassel and ear, is subtended by a bract so large that it completely envelops the spikelets and the ear resembles an ear of pod corn (fig. 1a).

Corn grass is another dominant mutant, discovered by Dr. Bailey Pepper in a field of sweet corn in New Jersey. It is now being studied by Dr. W. R. Singleton and it is with his permission that we cite his first report (1947). In the few plants we grew from seed supplied by Dr. Singleton, the bract subtending the paired spikelets is only occasionally found in the tassel. Many of the lateral in-

florescences have a superficial resemblance to the inflorescence of teosinte with its many spikes each enclosed by a single husk or bract. In corn grass many of the spikelets bear both stamens and pistils.

The position of the bract can be seen in a median longitudinal section of the teopod spikelet (fig. 1a). The bract originates directly above the hump which, with its horizontal vascular system, represents the node. The bract corresponds to the leaf sheath. Occasionally the leaf blade is present, just as in the husks there may be "flags." On the glume we have seen a part equivalent to the blade of the leaf only in a few plants of teosinte and *Tripsacum laxum* in which parts of the staminate spikelet proliferate. The spikelet resembles a bulbil in the inflorescence of an agave plant and a few of them produced small roots.

There are, however, many degrees of development of the part homologous to the ligule, the fringe at the tip of most glumes. An auricle is not present in the glumes unless there is also the part equivalent to the leaf blade. The fringes along

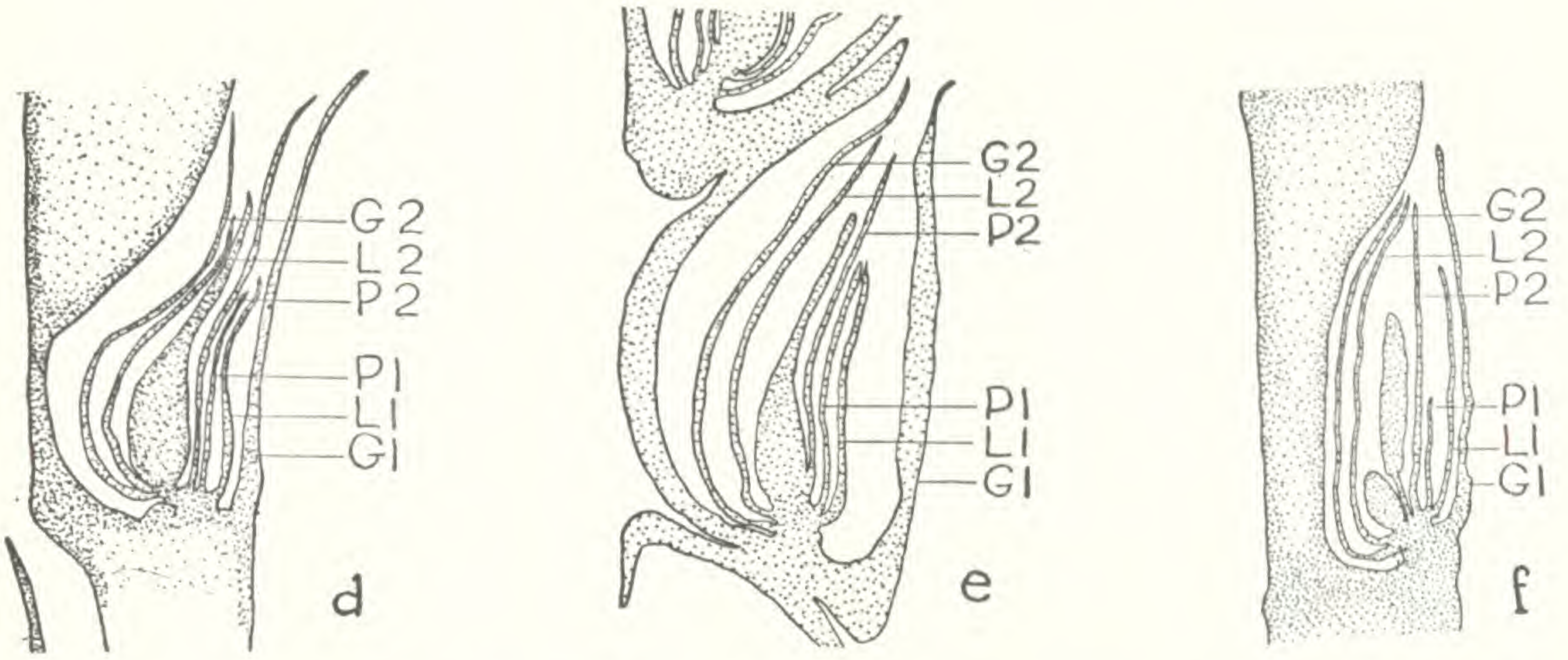

Fig. 1 (cont.). Median longitudinal sections through (d) lower or female portion of *Tripsacum* inflorescence, (e) of teosinte inflorescence, (f) inflorescence of *Manisuris cylindrica:* Br, bract; G1, lower or first glume; G2, upper glume; L1, lemma of first or lower flower; L2, lemma of second or upper flower; P1, palea of first flower; P2, palea of second flower.

the lateral margins of the glumes, lemmas, and paleas represent the margins of the leaf sheath. The keel of the bi-keeled lemma is often, but not always, the line of division between the margin of the sheath and the sheath proper. The sides of the lemma often have a vascular system, and this is lacking in the leaf-sheath margin.

At the base of the lower glume in the pistillate spikelet of the grasses we are considering is a line similar to that between the leaf sheath and the lamina of the usual maize leaf, but homologous to the junction of the leaf sheath with the node. This line is variable in width and color. It is not prominent in the staminate glumes.

We have been unable to find any color pattern of the pistillate glumes and the leaf sheaths which is associated with the glume bar or glume spot on the staminate glume, although this may be masked by other colors. This marking of deep

maroon or purple varies greatly in size, from a small dot to a patch of color covering the lower two-thirds of the maize glume. In most *Tripsacum* it is quite consistently a small spot or triangle.

The maize leaf sheath has prominent ribs marking the vascular strands. Between these one often finds hollows or pits, and there may be many hairs. These surface irregularities and hairs are found in many other grasses and recur in homologous parts of the plant. The most extreme surface irregularities are found on the lower glumes of *Manisuris*. Some of the glumes are so peculiarly sculptured that the forms have been given specific rank (*M. rugosa, M. corrugata, M. tuberculata,* and others), although it is doubtful if all of these should rightfully be considered species. The glumes of maize and *Tripsacum* are often sculptured, and while the sculpturing never reaches the extremes found in *Manisuris* and in *Hackelochloa granularis,* the irregularities are often accentuated by colored markings.

The hairs on the leaf sheaths of maize, teosinte, and *Tripsacum* are usually concentrated along the margins near the auricle. Hairs are usually inconspicuous on the female glumes but they are occasionally present in numbers proportional to those found on the leaf sheath. Some hairs are always present on the staminate glumes, and they may be abundant enough to give the glume a silky appearance. The hairs are nearly always unicellular and vary in shape from short and thick to long and slender.

The hairs which develop in the pulvinous notch, at the point of attachment of the leaf to the stem, or of the glume to the rachis, are often prominent in the maize ear. We have not been able to see material of the "corn cob fur" described by Richey (1946) and cannot be certain of the origin of the hairs in his specimen. From his photographs they appear to have a regular distribution and probably are an extreme development of the hairs on the margins of the rachis flaps, in the pulvinous notches, and those about the base of the rachilla of the spikelets. The description of the hairs, ". . . a tube with somewhat thickened walls . . ., few, if any cross walls, and they terminate in definite points, . . . extremely fragile," suggests this. It is far more likely than that they are "wild fibers from the vascular system." With the exception of some obviously fasciated forms, we have found nothing in the structure of maize for which a homologue could not be found, if not in maize, then in other grasses. All the obvious variations which distinguish tunicate, teopod, corn grass, and *ramosa* maize from the usual plants follow a definite pattern. In the case of structures described as "supernumerary silks from between the rows of grains," for example, these turned out to have a simple explanation. They were silks of partially developed lower flowers of the spikelets.

Glumes are generally smaller in South American highland maize. Not only are they smaller in the common varieties of maize, but in ears which have the tunicate character the enlarged glumes frequently do not cover the grains. This

is in contrast with North American ears which have the tunicate character, for these ears usually have glumes several times longer than the grain. The staminate glumes in South American tunicate plants often are only slightly longer than those of their normal sister plants. While some of the ears we collected might have carried the weak allele of tunicate described by Mangelsdorf (1948), small glumes were common in Dr. Brieger's crosses of pod corn and native South American corns.

While the smaller glumes in South American maize are probably due to several modifiers, there is a dominant gene, vestigial glume, which has been described by Sprague (1939). The original material was a single plant in a small planting of corn from the Belgian Congo. The glumes are greatly reduced, both in ear and tassel. Unfortunately the plant produces very little pollen because the anthers are exposed to the sun. This has made it difficult to produce a commercial sweet corn with the vestigial glume character.

Thick and hard plant parts are most prominent in plants which appear to have some tripsacoid influence, although the glumes and cobs of some Guatemalan Big Butt maize (Anderson & Cutler, 1942) and of Guarani flint from lowland South America are almost as hard as those of teosinte and some *Tripsacum*.

In ears of maize with only a few grains, all parts of the phytomers in which grains develop are hardened and have their usual colors, while the phytomers which do not develop grains are soft, flexible, and lack strong coloration.

LODICULES

Up to now we have been discussing structures which fall outside of the flower. If we consider the pattern for the monocotyledonous flower to be essentially that of the lily, the lodicules represent the remnants of the inner perianth whorl. The outer perianth whorl is absent. Usually only two lodicules are present, although Sharman (1939) has found some spikelets with three. The lodicules in maize, teosinte, *Tripsacum* and *Manisuris* are best seen shortly after the silks emerge or the day the flowers open to release the anthers. At this time the lodicules, which have swelled and thus forced the staminate flower open, are large and turgid. Even though the lodicules no longer function in the maize ear, they still become turgid at the proper time. In some of the highland Bolivian maize the lodicules were exceptionally large and had a definite vascular system.

STAMENS

Usually there are only three stamens in each staminate flower, but occasionally there are none, and sometimes two, four, or five. From their position in reference to the lodicules and to the three carpels, we know that the stamens represent only one, the outer, of two whorls of stamens of our pattern lily flower. In one specimen of maize with four anthers, the extra stamen arose between the two lateral stamens of the normal three and thus appears to represent one developed from the inner whorl of stamens. In the rather frequent staminate maize flowers with only two stamens, the remaining two were the lateral ones.

Although the stamens in the pistillate maize flowers are usually vestigial, they occasionally develop, especially when the plant is grown under peculiar conditions or is influenced by some gene with a strong effect, such as tunicate, or some tassel seed genes.

There is some variation in the diameter, length and shape of cross-section of the filament, but the most conspicuous variations in the stamen are in the anther. Colors vary widely and are related to colors in other parts of the plant. In size the anthers range from occasional minute ones (about 3 mm. long in one of our dwarf Paraguay crosses with Golden Bantam) to nearly 9 mm. (in an exceptional tassel of open-pollinated yellow dent). Most of the paired locules are cylindrical and round off suddenly at the ends but in some the ends are pointed. Although we have not seen anthers like those described as bearing the gene "warty anther" (Emerson, Beadle and Fraser, 1935), partially collapsed and partially functional anthers are common.

The pollen of maize is the largest in the grass family (Wodehouse, 1945) and is twice as large in diameter as wheat pollen. Some of our lowland Bolivian and Paraguayan plants had pollen grains which measured about 60 μ, just slightly larger than the largest wheat pollen, but most maize pollen grains are about 100μ in diameter. Markings on all the grains we examined are quite uniform.

Pollen of plants with the dominant gene, gametophyte factor, fertilizes 95 to 99 per cent of the kernels of plants with the gametophyte factor when it is in competition with pollen lacking the factor. Another gene, small pollen, governs the appearance of pollen that is smaller than usual. There are numerous male-sterille genes, most of them recessive, which control shrivelled or non-exserted anthers and non-functional or abortive pollen.

PISTILS

The three carpels of the grasses under consideration are united into a unilocular, one-seeded ovule. Of the vascular strands in the midribs of the carpels, only those of the two lateral carpels, the ones which do not bear the grain, continue into the style and the two branched hairy stigmas. Occasional plants of *Tripsacum* and maize have three stigmas. In maize the style is very short and the entire silk and the bifurcate tip is stigmatic. The length and thickness of the stigmas and the number and size of hairs on them vary greatly, not only in maize, but also in teosinte, *Tripsacum* and *Manisuris*. The color of the silk in these grasses is, like that of the anthers, related to colors in other parts of the plant.

SUMMARY

1. The grass plant is made up of units called phytomers, which consist of an axillary bud at the lower end, a section of the axis, and a leaf at the upper end.

2. Although the units are modified in the various parts of the plant, their parts are homologous, whether they are in the vegetative or reproductive areas of the plant. Therefore, changes in structure of any part of a unit are often repeated

in the other units. Homologies of the parts in maize, teosinte, *Tripsacum* and *Manisuris* are discussed.

3. A study of homologous variation is of value in plant breeding because it is often possible to identify plants carrying desirable seed characters by a study of the staminate parts or the stem. Plants which will be useful in crosses can be selected at the time pollinations are made.

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RIGHT-HANDED AND LEFT-HANDED CORN EMBRYOS

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The vertical stem of a corn plant, with its two rows of leaves arranged in a plane, has the appearance of a bilaterally symmetrical structure, but a close examination shows that this appearance is deceptive. The sheath of each leaf of such a plant is wrapped around the internode with its edges overlapping. If the observer imagines himself as standing in the position of the internode of the stem, with the leaf sheath around him like a coat, he will find that sometimes the right half of the sheath overlaps the left, and sometimes the left overlaps the right. For convenience we shall designate the one as dextral, or right-handed, and the other as sinistral, or left-handed. Further examination of the plant reveals that the dextral and sinistral leaves are arranged in alternate sequence along the stem. Thus it follows that the overlapped sides of the sheaths all fall on one side, and, if we should split the plant lengthwise in the plane of the midribs of its leaves, one half would have only the overlapping sides of the sheaths and the other would have only the overlapped sides (pl. 34).

This asymmetry of the shoot, which is characteristic of almost all grasses, is further shown in various species by other characteristics. Usually there is some difference between the two sides of the collar at the top of the sheath; the auricles, when present, ordinarily show some differences and alternately reverse their direction of overlapping in successive leaves; the leaf blade is frequently asymmetrical; and the insertion of the base of the sheath marks a spiral line on the stem. This structural pattern may be regarded as a sort of morphological dorsiventrality, but it is apparently not always correlated with orientation in rhizomes, stolons, or other horizontal stems.

Since the overlapping edge of the sheath is inserted on the stem a little lower than the overlapped side, it follows that the line of insertion of a right-handed leaf describes a left-handed spiral, and that of a left-handed leaf a right-handed spiral. This reversal of direction of the spiral at each node is an aspect of the phenomenon known as *antidromy*, which received much attention, especially from German morphologists, during the latter half of the nineteenth century. It occurs in one way or another in many kinds of plants and has been cited in objection to the theory that the distichous arrangement of the leaves of a grass can be interpreted as a form of spiral phyllotaxy (Elias, 1942, p. 29).

The significance of this reversal of pattern in consecutive phytomers has never been fully explained. As far as the grasses are concerned, it is only a part of a more comprehensive pattern in which various other structural differences appear in successive internodes. In some species, for example, the stem has alternately long and short internodes, the short ones sometimes being so reduced that the leaves appear to be opposite (pl. 34).

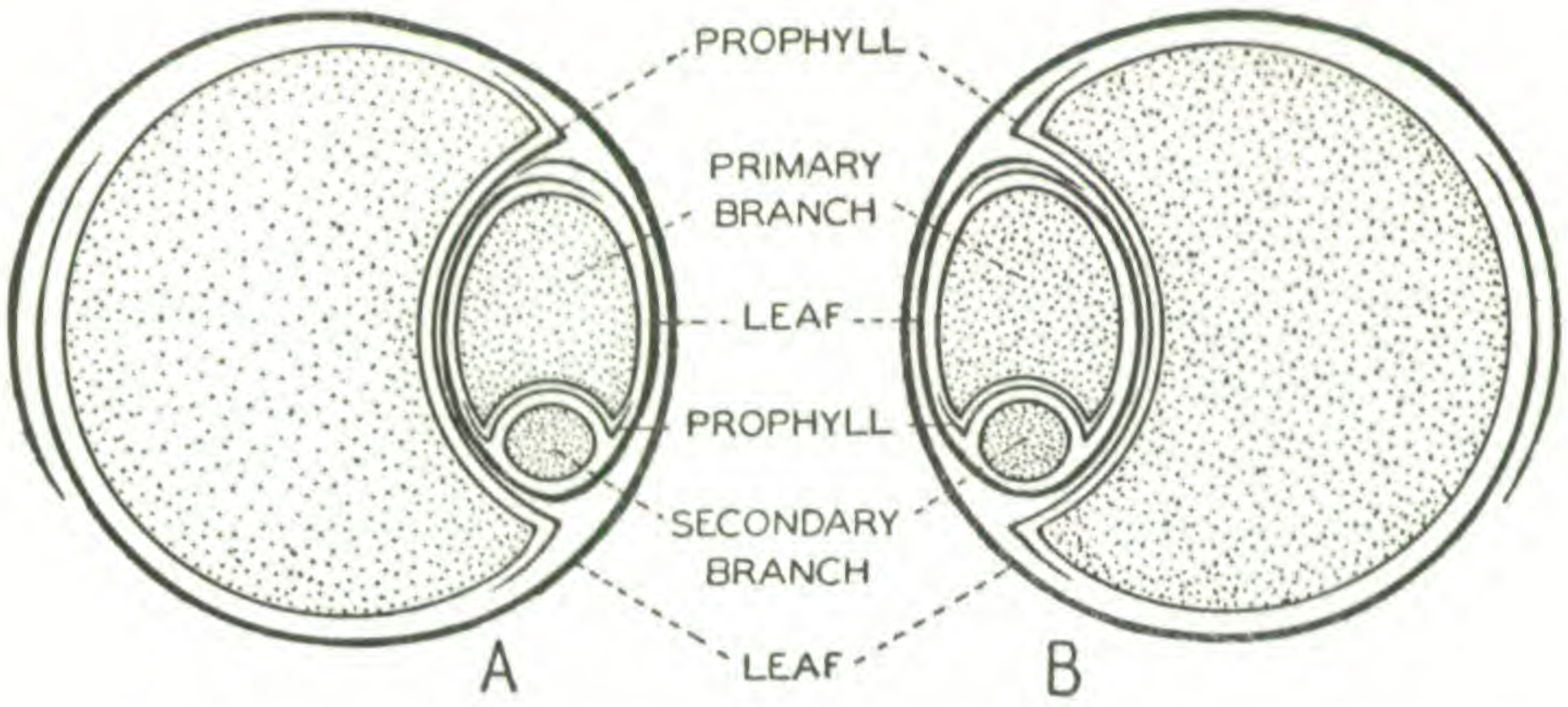

Fig. 1. Cross-sections of two consecutive internodes of a corn stem, showing leaves and axillary structures. A birdseye view of the structural pattern of the plant can be produced by superimposing one of these diagrams on the other. Note that the overlapping edges of the leaf sheaths are both on the same side of the stem and that the secondary branches both fall on the opposite side.

It is obvious that every individual grass seedling must start out in life as either a right-handed or a left-handed plant, as being determined by the direction of the overlap of the sheath of its first foliage leaf, the coleoptile being excluded from consideration. When a large number of embryos of any one species are classified as dextral or sinistral, the ratio is approximately 50:50. This can readily be demonstrated by examining the seedlings grown from a handful of corn.

When a branch arises in the axil of a leaf, its true foliage leaves (the prophyll excluded) fall in a plane which cuts at right angles the plane of the leaves of the main stem (fig. 1). The sheath of the lowest leaf of the axillary branch ordinarily overlaps in the same direction as that shown by the leaf subtending the branch; that is, right-handed branches arise in the axils of right-handed leaves and left-handed branches in the axils of left-handed leaves. To this there are, however, occasional exceptions.

Furthermore, the first leaf of a branch, with whatever axillary structure it may subtend, is located on the side of the branch next to the overlapped side of the subtending leaf of the main axis. From this there may result a peculiar picture in a grass which branches profusely. Suppose we have a vertical grass stem whose leaves stand in an east-west plane, with the overlapped edges of its leaf sheaths all on the south side. In the axil of each leaf there develops a branch, the plane of whose leaves extends north-and-south. Each of these primary branches produces a branch of the next order in the axil of its lowest leaf. All these secondary branches will then fall on the south side of the plant, producing at first a very asymmetrical structure.

This same pattern of asymmetry is carried into the inflorescences of many grasses as far as the branching of the various axes is concerned. Ordinarily nothing comparable with the regularity of the overlapping of leaf sheaths can be detected, for the simple reason that grass inflorescences seldom have bracts sufficiently

developed to overlap. It is generally conceded that at least the glumes and lemmas of the spikelet are reduced leaf sheaths, but they are usually not broad enough to encircle the rachilla and overlap.

Toward the close of the past century a number of interesting cases of antidromy were reported and discussed in a series of papers by George Macloskie (Macloskie, 1895, 1896, 1896a, 1896b). Many of the plants with which he deals are outside the grass family, and I have not examined them, but one observation on the structure of the ear of corn is obviously not plausible, and I have been unable to substantiate it by re-examining the material. The point in question is not one of great consequence, but it does involve an interesting fact. Moveover, Macloskie's statement has been cited in at least one later study (Elias, 1942, p. 29) and will, if not corrected, continue to lead to confusion. A refutation seems, therefore, to be in order.

The problem can best be presented by quoting the following extracts (Macloskie, 1895, pp. 379–380). The italics are mine.

> "It was then shown that . . . . . there must be two kinds of plants of every species of the order [Gramineae]; the one kind or 'caste' has its lowest foliage leaf . . . . . with the right margin of its sheath overlapping the left margin, 'dextrally infolded' as I term it; and the other caste has the left margin overlapping the right, 'sinistrally infolded. . . . . Thus it became manifest that as there are two castes of the maize plant, so there are two castes of grains, the one being the 'antidrom' of the other . . . . . ."
>
> "The ear consists of columns each containing a pair of rows of grains; we may designate the row opposite our right hand as dextral and the other row (opposite our left) as sinistral. It was soon made out that in the particular ear examined *the grains of the dextral row were all with dextral embryos, and those of the sinistral row had sinistral embryos.* Whether this law would apply to all the ears on one plant, or whether the order would be inverted between the ears arising from successive nodes, or between the ears of different plants, is yet to be determined. On examining the very young ear of maize I found the grains of the paired rows of each column oriented close to each other, almost face to face, the young styles running up together, and a gap between the adjoining two-rowed columns.
>
> "From this discovery the inference was obvious that the seeds of corn differ from each other antidromically, *according to the side of the placenta or axis from which they arise; that their embryos vary in consequence, and determine the caste of the future plant.*"

From the above it is obvious, in the first place, that Macloskie was confused in his understanding of the morphology of the ear of corn. A pair of rows of grains is not at all the morphological equivalent of two rows of seeds attached to a linear placenta. Furthermore, on theoretical grounds, I have for many years questioned the accuracy of his observation. Granting that the general antidromic pattern of vegetative structure of a grass plant is as described, there still seemed to be no plausible reason why it should affect the pattern of the embryo. The characteristic pair of grains of corn is borne in two separate spikelets on a short branch arising from the side of the cob. These two spikelets, representing secondary branches on this short primary branch, might be expected to reflect the normal antidromic vegetative pattern even though this be difficult to detect. But why should the pattern continue into the embryos, which are entirely separate morphological entities?

Macloskie seems to have had some misgivings about his thesis and leaves the way open for amendment in the light of further study. As far as I have been able to learn, no later report was ever made. He does not indicate how many pairs of grains he examined, but the number must have been small. Over a period of some five or six years we have from time to time examined individual ears of a dozen or more varieties from widely separated localities, and in not one of them have we found verification of Macloskie's statement. In practically every instance, the examination of only two or three pairs of grains was sufficient to refute it.

In the early studies, the ear selected was held with its tip up, and grains from the left and right rows of a pair were removed and planted separately. The following classification of embryos represents a combination of the results secured from several pairs of rows of a commercial dent variety. It is typical of the results from several ears studied in this way.

Sinistral embryos in grains from left row	114
Dextral embryos in grains from right row	128
Dextral embryos in grains from left row	121
Sinistral embryos in grains from right row	111

It will be noted that only those embryos of the first and second categories, approximately 50 per cent of the total number, conform with Macloskie's statement. The other two classes should not have occurred at all.

But the error as to the structural pattern of the individual *pair of spikelets* is really greater than indicated above. This is disclosed by a comparison of the right and left grains of individual pairs. Paired grains were planted side by side, and the paired seedlings fell into the following classification:

Pairs with left embryo sinistral and right dextral	95
Pairs with both embryos dextral	130
Pairs with both embryos sinistral	95
Pairs with left embryo dextral and right sinistral	104

Of these four classes, only the first, approximately 25 per cent of the total number, conform with Macloskie's statement. The second and third classes may be said to be half right as far as individual grains are concerned, but wrong as an expression of the pattern of the pair. The third class is entirely wrong.

From these observations it is evident that the type of embryo—sinistral or dextral—is determined solely by chance. It is in no way correlated with the position of the grain in the typical pair of spikelets.

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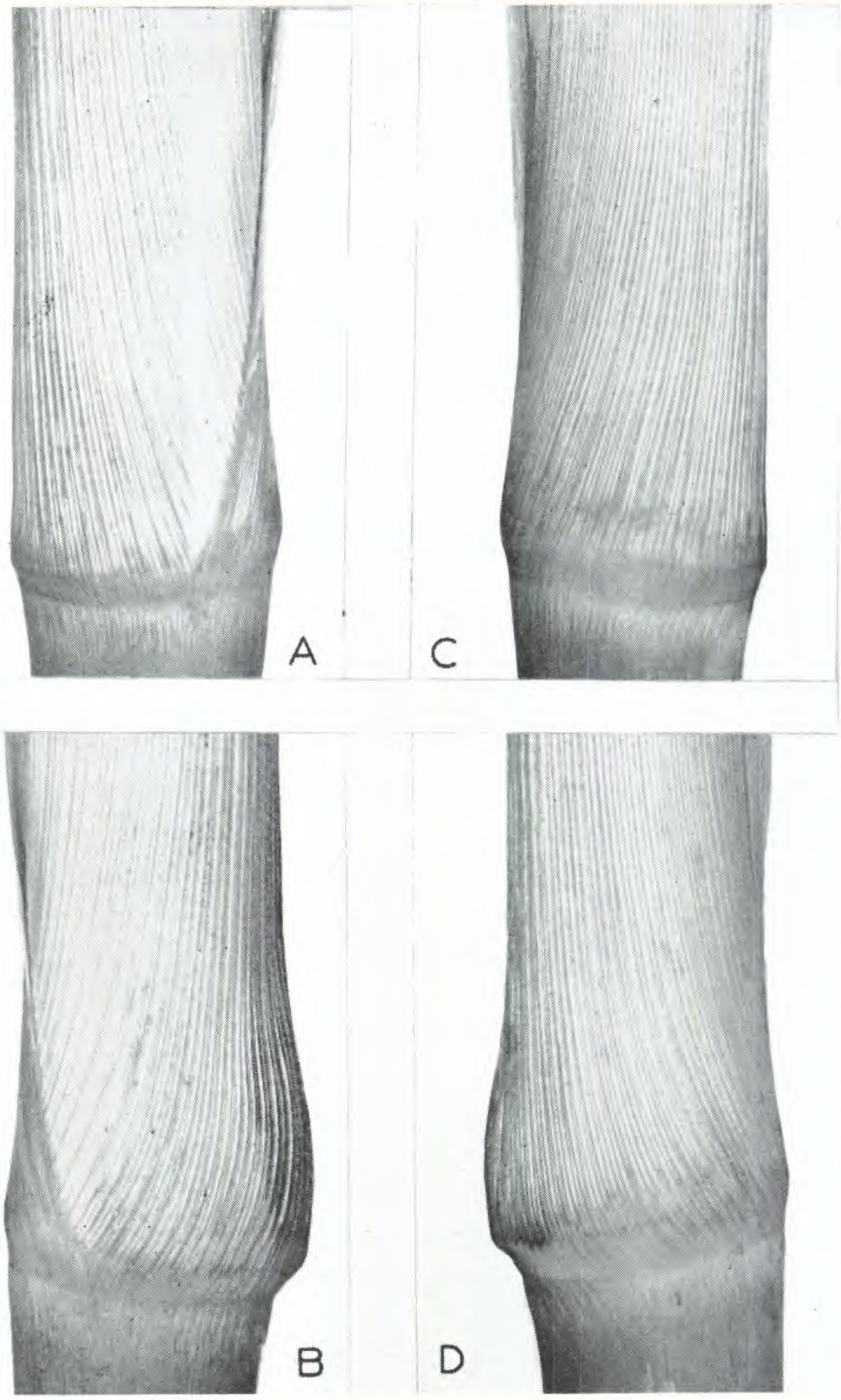

WEATHERWAX—RIGHT- AND LEFT-HANDED CORN

Fig. 2. *A* and *B*, two consecutive nodes of a corn plant, as seen from the same side of the stem. Note that in *A*, the left side of the sheath overlaps the right, and that in *B* the overlap is in the opposite direction. In *C* and *D*, the same nodes are shown from the other side of the stem.

3

4

WEATHERWAX—RIGHT- AND LEFT-HANDED CORN

Explanation of Plate

PLATE 35

Fig. 3. Part of a plant of St. Augustine grass *(Stenotaphrum)*. The appearance of opposite leaves and opposite branches, which is unusual in grasses, is due to the alternate sequence of long and very short internodes in the stem.

Fig. 4. Paired grains on an ear of corn. In *A* the paired rows of grains are connected by the curved lines at the top. *B* and *C* show pairs of grains from the upper and lower sides, respectively. Since the two spikelets which produce the pairs of grains are consecutive lateral branches on a short primary branch, *they* might be expected to show antidromical patterns, but there is no reason why such patterns should extend into the embryos of the grains. Examination of the embryos shows that their pattern is determined by chance and not by the position of the grain in the pair of spikelets.

A MORPHOLOGICAL ANALYSIS OF ROW NUMBER IN MAIZE

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The kernels of an ear of maize are usually set in longitudinal rows of from 8 to 30 or more. Certain genetic stocks, and an occasional ear in open-pollinated varieties, may have only 4 rows. For numbers much above 30, the kernels are so crowded that the rowing is obscure; various irregularities may modify or conceal the row pattern (Weatherwax, 1916, 1917), but in most of the varieties of *Zea Mays* the kernels over a good portion of the ear are arranged in definite and usually conspicuous rows. In nearly all varieties the row number is even, since the kernels arise from paired spikelets which are themselves disposed in regular rows (Collins, 1919).

The history of row number is apparently complex. Both in South America and in the southwestern United States archaeological investigation has demonstrated that the earliest varieties had 12 or 14 rows (Bird and Anderson, in press), and Bird's recent excavations indicate that this condition persisted unchanged for a long period. Both in South America and in the southwest 8- and 10-rowed varieties appeared at a later date (Carter and Anderson, 1945). Another type of change in row number has been associated with the dent corns of Mexico. Since at least the times of the Toltecs, row numbers of 16 and above have been characteristic of central Mexico (Anderson, 1946), and it is apparently chiefly from that center that they have been so widely spread around the world as to characterize many of the world's centers of commercial corn production.

Since the early days of studies upon inheritance in *Zea Mays* (Emerson and East, 1913) it has been apparent that the genetic basis for differences in row number is complex. Extensive and careful studies were carried on by the late R. A. Emerson and his students and collaborators for several decades. While he made a number of preliminary and informal reports his results in different crosses were rather contradictory and have not yet been formally published. Lindstrom (1929, 1931) observed linkage between genes for row number and genes for pericarp color.

The morphological bases for differences in row number are difficult to study upon the ear itself, an organ so modified that its exact relation to other grass inflorescences is still a subject for research and so highly vascularized that such research is technically difficult. Accordingly, for the past decade, we have carried on a comprehensive survey of variation in both the ear *and* the tassel (the male and female inflorescences). As Bonnett's (1940) developmental studies have clearly shown, these two inflorescences are scarcely distinguishable morphologically in their early stages but beyond a certain point the ear becomes progressively harder and thicker, the tassel progressively more lax and expanded. From modern

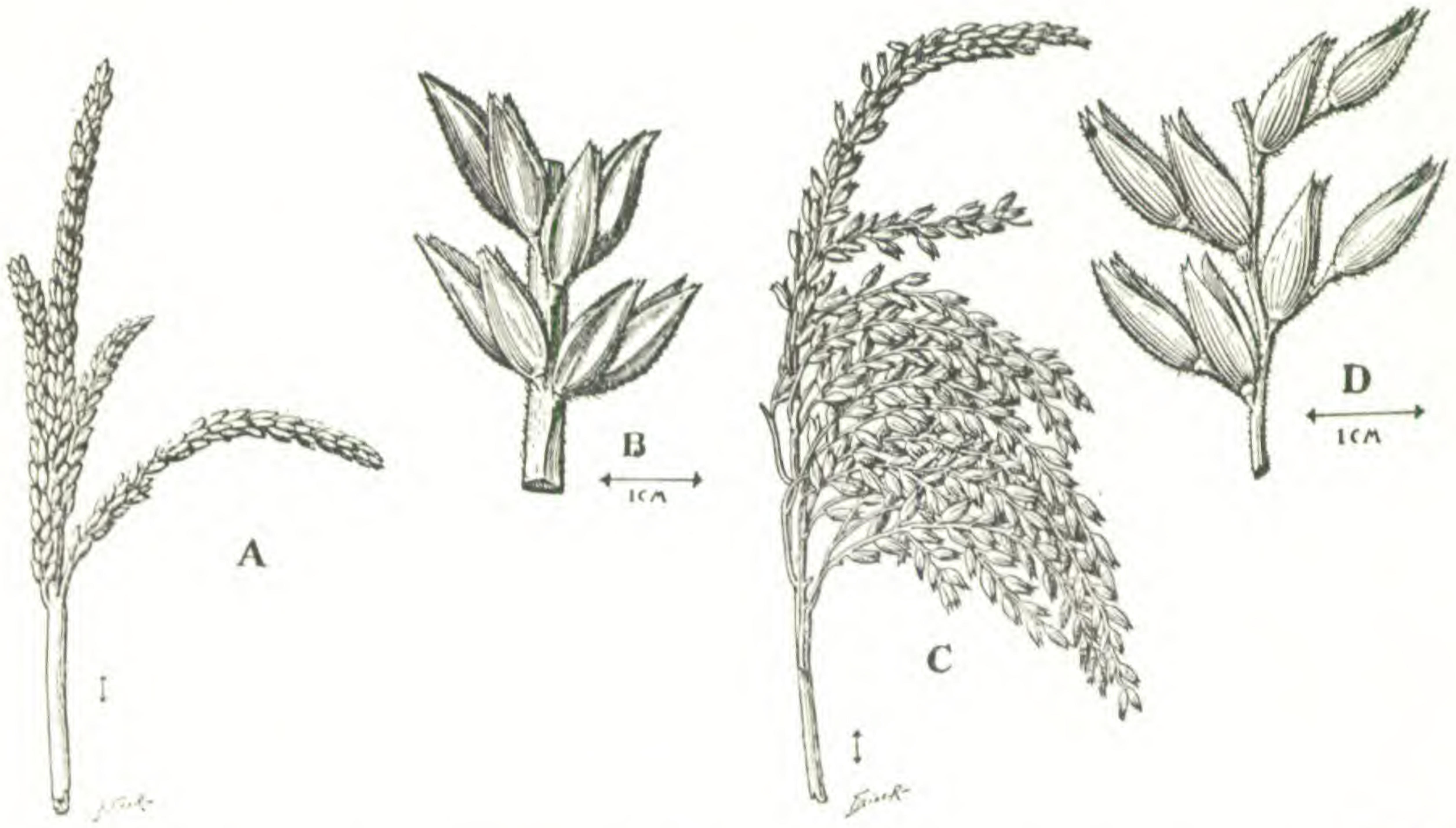

Fig. 1. Two extreme tassel types from an inbred plot. *A* and *C* show the general habit of the tassel. A few branches have been removed from *C* as indicated in the drawing, to reveal the structure of the tassel. *B* and *D* show equivalent portions of the lowest tassel branch from *A* and *C*. The arrow under the figures is 1 cm. in length. Condensation in *B* is 2.0, in *D*, 1.0.

genetic theory we know that the germinal differences between various types of ears will also be operating in the tassels of those same plants. Since the tassel is an expanded and relatively unmodified organ, changes which are difficult to determine and equally difficult to interpret when viewed only in the ear are easier to score and simpler to understand when studied in the tassel. Therefore, though this paper is primarily an attempt to analyze variation in the ear, we must first consider the morphology of the tassel with reference to its pattern of variation.

Though the tassel (like all other parts of the corn plant) varies greatly from one strain to another, its basic plan is singularly uniform. It is composed of a central axis with a varying number of secondary branches, terminated by a dense portion which has generally been referred to as the central spike. The secondary branches may themselves be branched, particularly the lower ones, and in some kinds of maize there may even be branching of the fourth and fifth order.

The fundamental unit of the tassel is the spikelet, technically a condensed raceme. It is about a centimeter long and has two chaffy basal glumes which cover and conceal the remainder of the spikelet except for a short period during anthesis. In *Zea* the spikelets of the tassel are almost universally borne in pairs, one of which is practically sessile, the other being noticeably (and oftentimes conspicuously) pedicellate (fig. 1). This condition characterizes not only *Zea*

but nearly all of the genera in the two tribes of grasses (Maydeae and Andropogoneae) with which this genus is obviously most closely related.

In modern maize one of the most conspicuous variables in tassel structure is the arrangement of the spikelet pairs. In the wild grasses related to maize these arise one pair at each node, and in South America and in the Orient there are wide areas in which all the varieties of maize are so characterized. In the maize of central Mexico, however, this fundamental pattern has been so greatly altered as to be almost unrecognizable in its extreme manifestations. Since it was apparently from this center that most of the dent corns of commerce were ultimately derived, these same anomalies, in a somewhat diluted form, are to be found in all the areas of commercial corn production where dent corns play a dominant role.

Superficially, the Mexican dents (and associated rice popcorns) are characterized by compact, clubby tassels, densely set with spikelets. This condensation is equally true of the central spike, and of all the secondary and tertiary branches. When the spikelet arrangement on the secondary branches is examined in detail, it is evident that the dense effect is due to a kind of fasciation or telescoping of successive nodes. This telescoping may be of various intensities. In some commercial United States varieties it affects only a portion of the nodes. In such varieties the majority of the nodes will bear a single pair of spikelets, but a few may have two or more pairs. The most extreme manifestations of this tendency are seen in such kinds of maize as the short-eared many-rowed dents from central Mexico to which Anderson and Cutler (1942) have given the name of Mexican Pyramidal, and in the closely related rice popcorns such as Japanese Hull-less. In these varieties there may be no normal nodes along the whole length of the tassel branch, and the average number of spikelet pairs per apparent node may be four or five. (We say apparent node since there are various reasons for believing that the node number itself has not been primarily affected and that the peculiarities of these kinds of maize are due to a telescoping of successive internodes so that what seems to be but a single node with several pairs of spikelets is in reality a succession of nodes virtually on top of each other, each with its own pair of spikelets.)

This telescoping of the inflorescence has been designated as "condensation" (Anderson, 1944). Its effect can be seen throughout the tassel and it might conceivably be measured in the central spike, or on all or on one of the secondary tassel branches. Experience has shown that the most consistent results are obtained when it is scored on the lowermost secondary branch. (When, as in certain inbred strains, the lowest tassel branch is manifestly malformed, the next branch above is chosen for scoring.) Condensation is scored by recording for the central portion of the branch the ratio between the number of pairs of spikelets and the number of apparent nodes. (For precise directions see Anderson, 1944). This ratio runs from 1.0 in the uncondensed varieties of South America and of the Orient, to 4.0 and higher in Mexican dents and in certain inbred lines which resemble them.

As soon as the phenomenon of condensation had been recognized it was obvious that there was a close connection between condensation of the tassel and high row numbers of the ear. All maize varieties with row numbers of 16 or above were, without exception, found to exhibit condensation in the tassel. Eight-rowed varieties, without exception, were found to have no condensation. By utilizing inbred lines to minimize the effects of environmental variation it was possible to demonstrate that the over-all relation between row number in the ear and condensation of the tassel is so exact that it may be expressed in a mathematical equation. If we let C represent the condensation ratio, and R the number of rows on the ear, then these two variables are related in the following way:

$$R = 10C.$$

The relationship has been tested with a wide variety of material,—United States open-pollinated varieties, inbred lines derived from these varieties, Mexican varieties, Guatemalan varieties, popcorns, sweet corns, etc. The exactness of the correlation depends upon the variability of the stock which is being examined. If, as in the original investigation, one grows twenty or more plants of various inbred lines under optimum conditions, choosing a characteristic tassel from each inbred line, and a well-developed ear, then the correlation will be very high. There are a very few inbreds in which condensation of the tassel is not accompanied by a corresponding increase in row number, but they are very much in the minority as fig. 2 demonstrates. If open-pollinated maize is grown, two or three plants to a hill, and then the condensation of each tassel is correlated with the row number of each ear, the correlation is quite naturally less exact, but it is still clearly demonstrable.

In the commercial dent varieties of the United States there is an interesting variation in this correlation which has a logical basis. In Mexico the relationship between condensation and row number approaches a simple straight-line (Wellhausen, Roberts and Lenz). In United States dents the relationships between these two variables is curvilinear as shown in fig. 2. In other words, in North American maize a tassel may indicate an exceedingly high degree of condensation, yet the row numbers will be only in the lower 20's instead of in the 30's. This is probably due to the intense selection for ears of 18 to 22 rows which took place for several decades under the influence of the corn shows. The corn-show ideal called for an ear of 18 to 22 rows, but discriminated highly against ears with higher row numbers. During this period modifying genes which would have held down the expression of high condensation in the ear would have been at a selective advantage. The differences between scatter diagrams for tassel condensation vs. row number in Mexico and in the United States suggest that such modifiers are common in United States varieties. Further evidence for such modifiers was obtained from crosses between the two common inbred lines, WF-9 and 38-11, with Japanese Hull-less popcorn, a variety with a very high row number and extreme condensation. F-2's of 125 plants each were grown and scored for row number

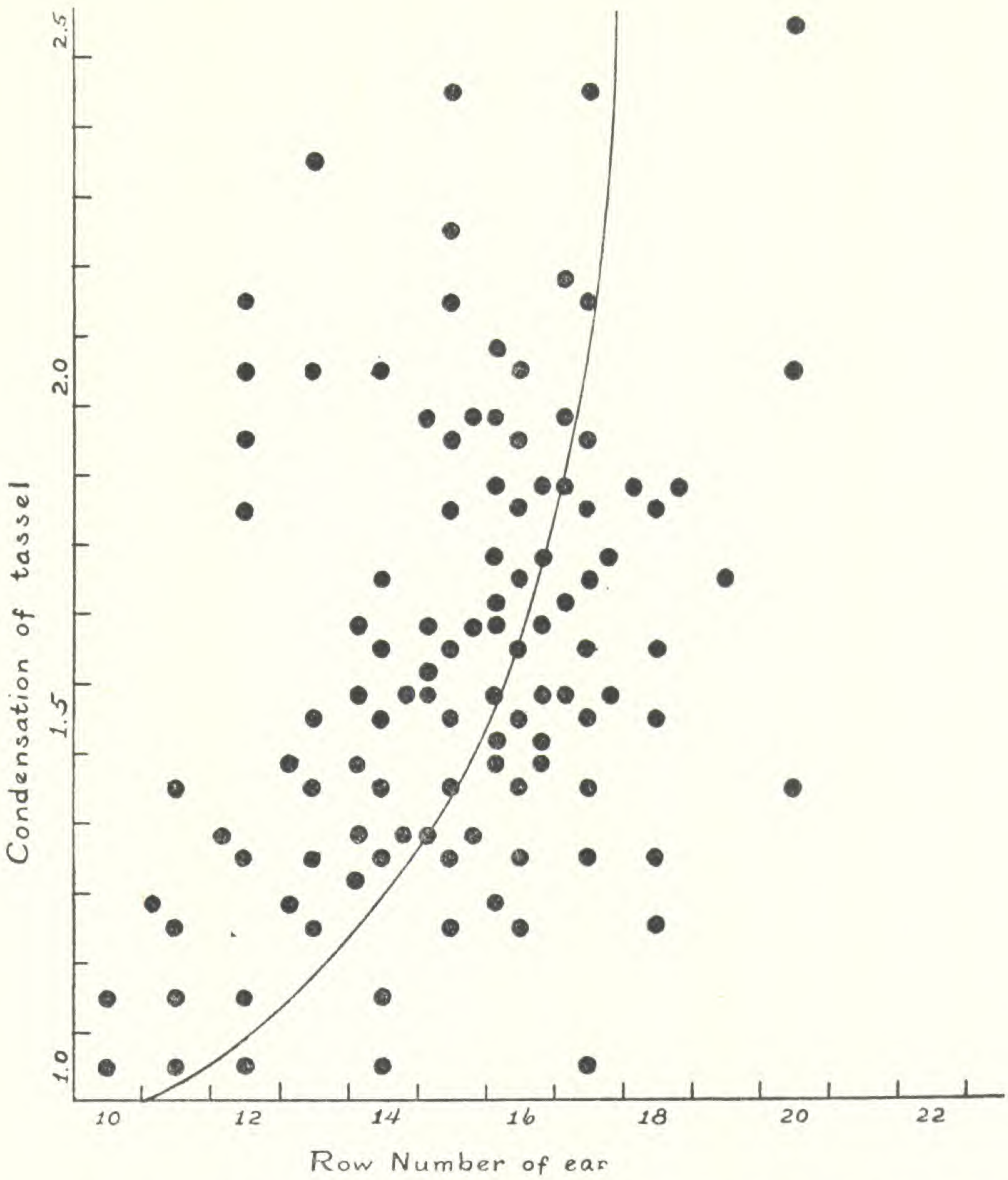

Fig. 2. Scatter diagram showing relationship between condensation and row number in 109 inbred lines. Condensation was scored on three tassels and averaged. Row number is the average of all the plants bearing well-developed ears (usually about 10.)

of the ear and condensation of the tassel. In each cross, row number of the ear and condensation were strongly correlated but extreme condensation of the tassel was not accompanied by row numbers of 30 or 40 as in the popcorn. Furthermore, this restricted expression of condensation was stronger in the cross with WF-9 than in that with 38-11. It was even greater in an F-2 between 38-11 and WF-9 than in the crosses with Japanese Hull-less. These results indicate that corn-belt maize does carry modifying genes which hold down the expression of condensation in the ear and that there are more such modifiers in WF-9 than in 38-11.

If condensation of the tassel is to be used as a precise indication of row-number potentiality, it must, however, be carefully determined. Since the first paper

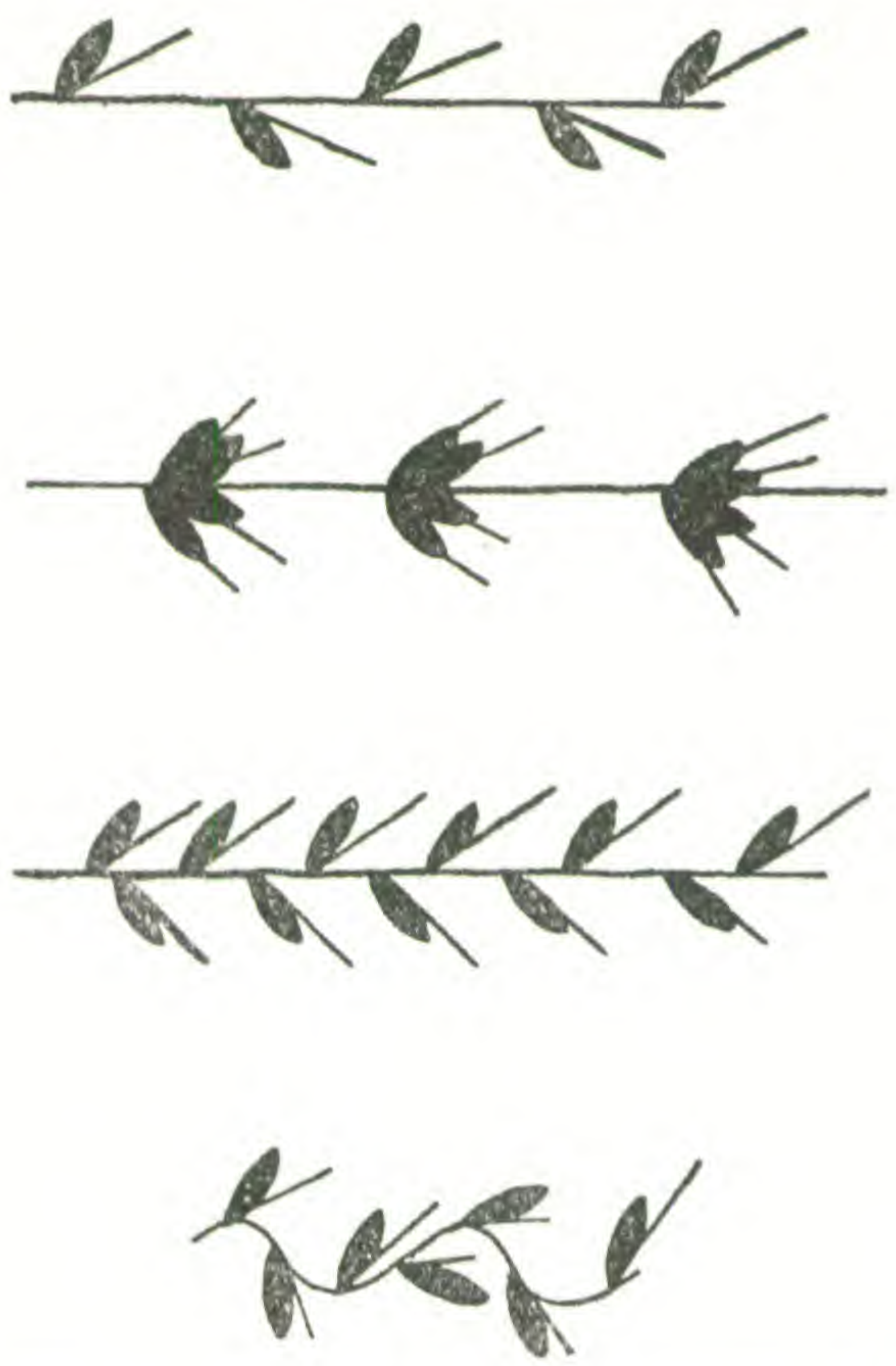

Fig. 3. Diagram showing various arrangements of the spikelet pairs on secondary branches of the tassel. In all four diagrams only the pedicel of the pedicellate spikelet is shown. From above to below: normal; highly condensed; short internodes; spiralled axis. Although the lower two produce thick-looking tassels which are superficially similar to those with condensation, their thickness is due to fundamentally different phenomena and has no effect upon row number.

(Anderson, 1944) on this subject some workers have attempted to lessen the tedium of tassel examination node by node. They have instead measured the density of the tassel in some such way as number of spikelets per centimeter of length. Though condensation does indeed produce a dense tassel, there are numerous other variables which may produce dense tassels without affecting the row number, as, for instance, short internodes or a spiraled axis (fig. 3). While it is true that after one understands the effects of condensation he can often estimate the row potentialities by merely glancing at a tassel in the field, it is equally true that in any precise investigation of the phenomenon it must be accurately determined according to the original directions.

Another abnormality of the inflorescence which affects row number has been described as "multiplication" by Cutler (1946). It apparently causes the bifurcation of the spikelet at a very early developmental stage so that two spikelets are produced instead of one. A high degree of multiplication is difficult to distinguish from a high degree of condensation, but lower grades are readily distinguishable in the tassel. In condensation the spikelet pairs tend to be regular, but successive pairs are arranged practically on top of each other. In multiplica-

tion the arrangement is normal but either or both of the spikelets within the pair is doubled. The effects are also different on the ear. Condensation produces ears in which the row rumber has been increased but in which the rowing is still regular. Multiplication adds additional kernels in a more or less crowded irregular fashion until the regularity of the rowing is no longer apparent. Extreme multiplication is rare in the United States and in Mexico, common in certain kinds of Guatemalan maize, particularly the yellow flints of the mountains, and is common in parts of South America. Its expression is most readily studied in what would otherwise be an 8-rowed variety. With a little multiplication there are occasional diamond-shaped kernels squeezed in between the regular rows. This is a common condition in flints of the northeastern United States. With a further development of the phenomenon there are so many of these extra kernels that the ear is divided into four quadrants, each representing two original rows. Within each of these quadrants the rowing is difficult or impossible to make out. With still further multiplication, the entire ear is so crowded with kernels that it can no longer be considered to possess a definite row number.

In the earliest stages of our investigation Dr. G. Ledyard Stebbins pointed out, from his wide knowledge of the Gramineae, that such phenomena as condensation and multiplication represent obvious teratological variations which have been selected under cultivation because they increase the row number and hence the productivity of the crop. Continued study has confirmed the soundness of his judgment. Nothing like either multiplication or condensation is characteristic of any of the wild-growing Gramineae. Furthermore, the extreme manifestations of condensation, such as are seen in certain inbreds or in an occasional ear from an open-pollinated variety of dent corn, are clearly fasciated. In the prehistoric remains of maize from the American southwest these fasciated extremes seem to have been more frequent when highly condensed varieties were first introduced into that area than they now are. This would suggest that the condensed varieties have gradually accumulated a set of modifiers which allow condensation to increase row number but tend to prevent the production of extreme, fasciated ears.

Therefore, if we are to study the variation pattern of the central spike, it would seem a good working hypothesis to confine our attention to varieties which are without either condensation or multiplication. It is clear that condensation affects this part of the tassel but it produces such thickly set spikelets that all other variation is obscured. To understand the basic variables one must concentrate upon non-teratological strains; in other words, upon maize which is without either condensation or multiplication.

VARIATION IN NON-TERATOLOGICAL MAIZE

If in this way we exclude the effects of condensation and multiplication, variation in the central spike is simple. All of the maize we have examined then falls in two extreme classes and intermediates between them. The 8-rowed varieties have the spikelet pairs of their central spikes in whorls of two. The 12-

Fig. 4. Measured diagram showing spikelet arrangement in 8-cm. portions of two central spikes. Left, from a 12-rowed flour corn from the Southwest. Right, from an 8-rowed northern flint. Scale in cms. Further explanation in the text.

rowed varieties have their spikelet pairs in whorls of three. In the 8-rowed varieties, as for instance in the older varieties of flints of the northern United States, the spikelet pairs are opposite and decussate. That is, if the pairs at any one node are set east and west, those at the next node are north and south, then the next pairs east and west, etc. Looking down the spike from the apex there will be spikelet pairs on four sides of the central spike, making 8 rows in all. The 8-rowed ear has an 8-rowed central spike.

Similarly in 12-rowed varieties without condensation or multiplication, if the whorl of 3 pairs at any one node is represented by positions 2, 6 and 10 on the face of a clock, then at the next node we shall find positions 12, 4 and 8, then 2, 6, 10 again, and so on. Looking down the central spike from the apex we shall see spikelet pairs on six of its sides, making 12 rows of spikelets. The plant with a 12-rowed ear has a 12-rowed central spike to its tassel. The complete homology between the two organs is as simple as that. Figures 4 to 6 show spikelet positions as actually measured on representative central spikes. The measuring was done according to the method originated by Mangelsdorf (1945) but the results have

been plotted on a scale of approximately equal value horizontally as well as vertically. The central spikes were examined under a dissecting microscope with a wide field. Accuracy was increased by having an assistant record the measurements. Several centimeters of the spike (usually a half to a third of its entire length) were chosen for examination. A mark is made with dye or ink at the precise spot where the measurements begin. The distance from each spikelet pair to this base line is recorded in millimeters, using a steel rule or calipers. Any one of the pairs at the base is chosen to begin with, and all the pairs which are on the same side of the spike are recorded in succession up the spike, removing each pair as it is measured. In some varieties there are ridges on the rachis which make it a simple matter to follow any one rank of the spike. In others the relationship is obscured, and one has more or less arbitrarily to choose a line of spikelet pairs. These pairs are then plotted to scale on cross-ruled paper, and successive vertical ranks to the right and the left of the original rank are measured until no spikelets remain on the portion of the spike chosen for study. The resulting graph is essentially a cylinder which has been cut down one side and flattened out into one plane. In attempting to make such an examination it is best not to begin with the more complicated types. An 8-rowed sweet corn or a northeastern flint will demonstrate how simple the arrangement can be and experience with it will aid one in interpreting the more complicated spikes of the dent corns.

Figure 4 demonstrates that, in the strict sense of the word, the arrangement of the spikelet pairs on the central spike is not in spirals as has been so frequently reported (as, for instance, in our own earlier papers on the subject). The pairs are clearly in whorls. In 8-rowed varieties they are in whorls of two, in 12-rowed varieties in whorls of three. In both of these sorts there is a regular alternation of whorl position so that the spikelet pairs can be followed in regular spirals in either direction, but this is not a spiral arrangement in the strictest sense. It is condensation which has obscured the simplicity of this regular whorling. With a low degree of condensation the whorling can still be made out from the scaled diagram though it is often difficult to determine from inspection. With a higher degree of condensation, the spikelet pairs are so thickly set upon the central spike that it is difficult or impossible, even from the diagram, to determine what the fundamental pattern may have been.

THE DETERMINANTS OF ROW NUMBER IN THE MAIZE OF THE UNITED STATES

Condensation and number of spikelet pairs per whorl are therefore the two main variables which determine row number in the maize of the United States. Multiplication, particularly in its lower grades, is occasionally met with, but it plays nowhere near the role it does in Guatemala or in South America. Since it may lead to irregular rowing and since the commercial varieties of the United States have been very strongly selected for straight rows, it is possible that its frequency may have been greatly reduced by this intense selection.

Figure 5 demonstrates how number of spikelet pairs per whorl and condensation interact in determining row number in the maize of the United States. Condensation is diagrammed on the vertical axis from the grade of 1.0, where there is no condensation and there is merely the normal pair of spikelets at each node, to the grade of 3.0, where there are on the average three spikelet pairs at each node. The horizontal axis shows the fundamental whorling of the central spike (and therefore of the ear as well) from whorls of two pairs at each node through various intermediate stages to whorls of three at every node. The numbers on the Cartesian surface show the row numbers to be expected with various combinations of these two tendencies.

For the interpretation of row number and particularly for its genetic analysis the most important fact demonstrated in fig. 5 is that for row numbers above 8 there are two quite different kinds of plants which can yield any row number. Take 12 rows, for example. They are to be expected on a plant with no condensation and with a central spike in whorls of three. They are equally likely on a

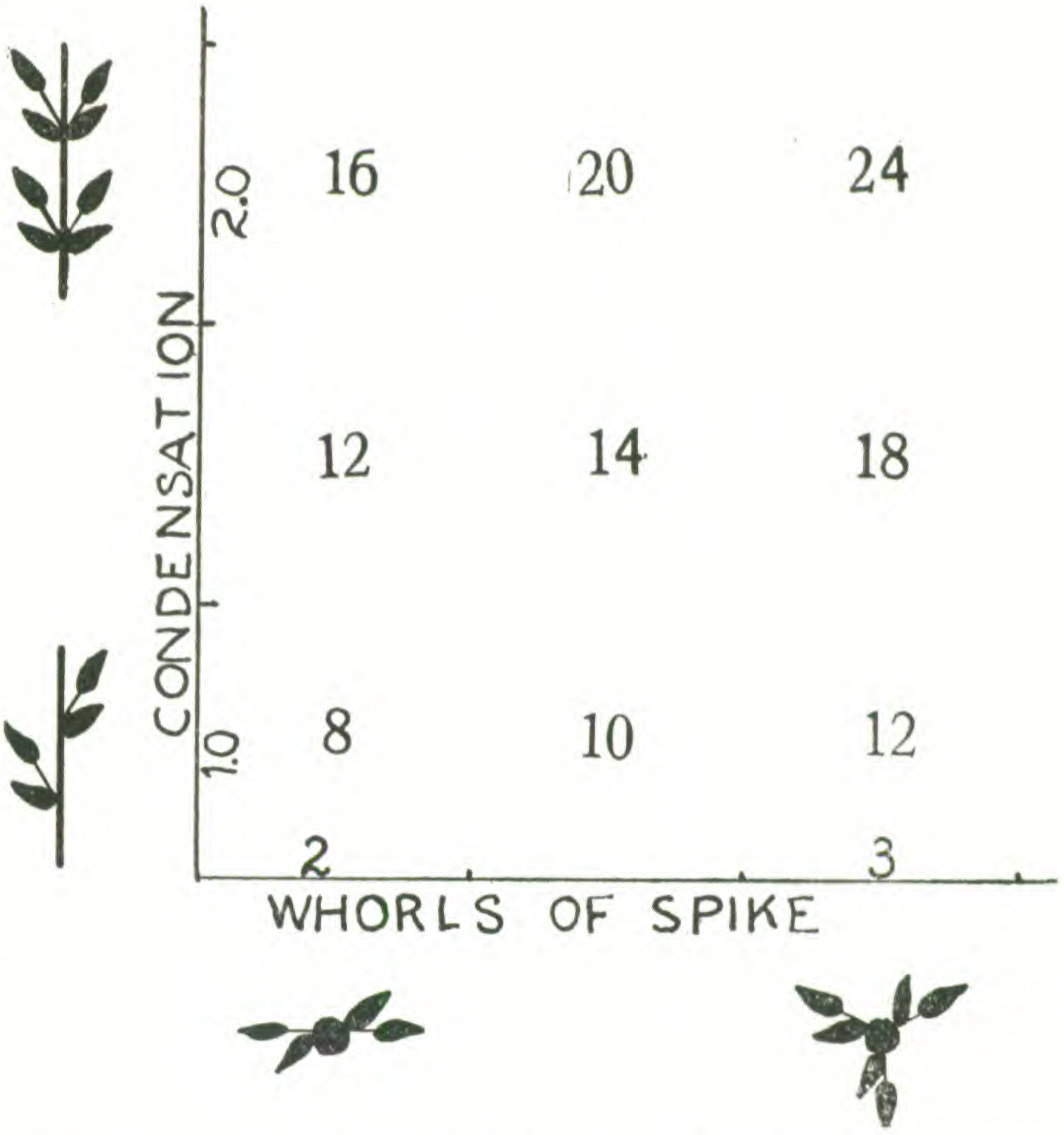

Fig. 5. Diagram showing how whorling and condensation interact in affecting row number. Whorling, from whorls of 2 pairs to whorls of 3 shown on the horizontal axis. Condensation from 1.0 to 2.0 shown on vertical axis. Numbers in the center show row numbers to be expected in the absence of modifying factors or other phenomena such as multiplication.

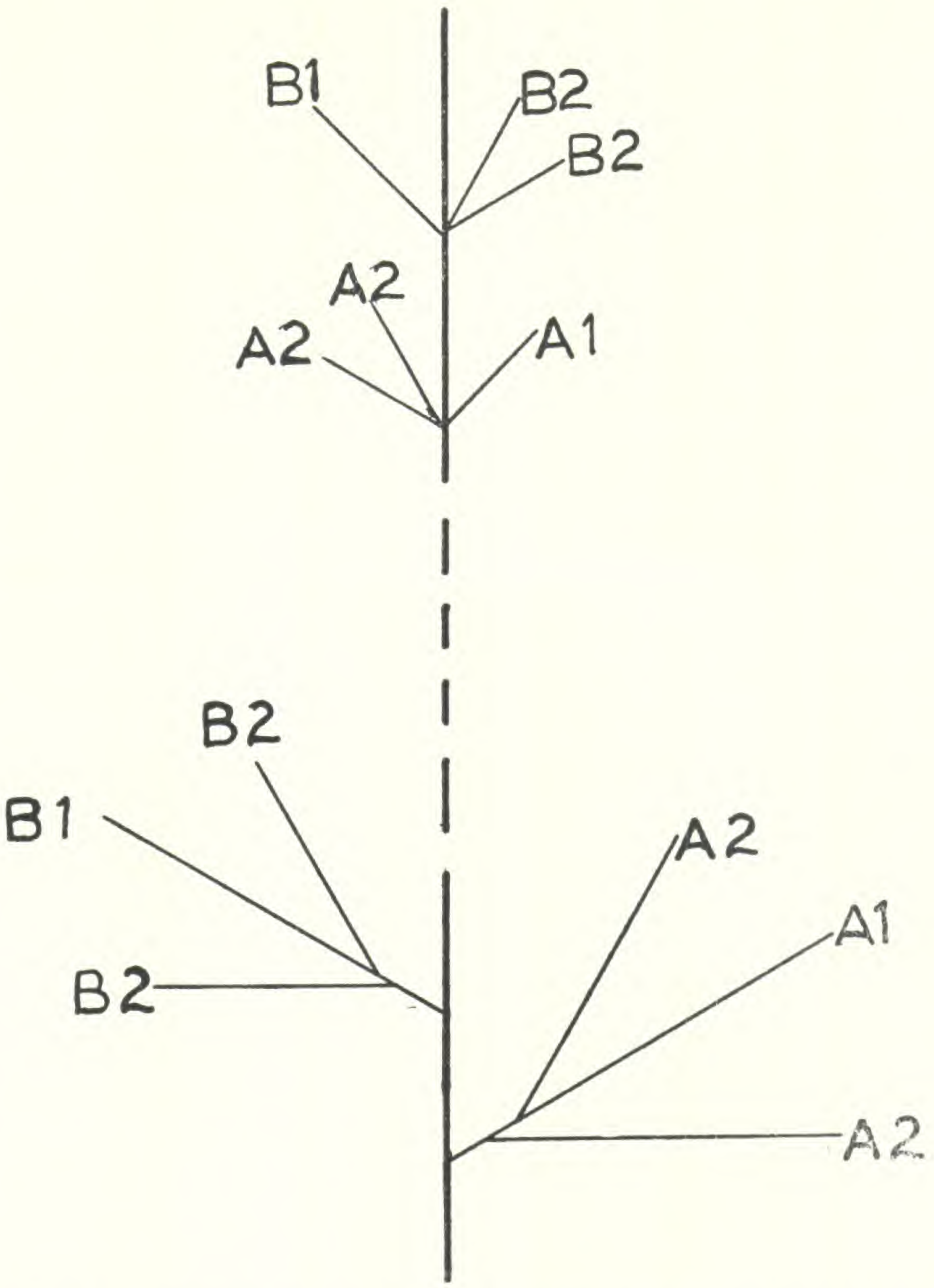

Fig. 6. Diagram illustrating possible relationship between the distichously arranged lower branches of a maize tassel and the whorled upper branches and central spike. Two lower branches are shown, each with its own axillary branches. At the upper nodes two such branches would be represented by two whorls of three. Each whorl takes the place of a primary branch and its two axillaries.

plant with whorls of two but with condensation of grade 1.5. Furthermore, these two types could be distinguished by examining their tassels. In the first type the arrangement of spikelets would be regular throughout, and the central spike would be in whorls of three. In the second type about half the nodes on the lowest secondary branch would have an extra pair of spikelets. The whorls of the central spike would be in two's, somewhat obscured by the disturbance of the spikelet pattern brought about by condensation.

THE INHERITANCE OF ROW NUMBER

The completion of the morphological analysis outlined above makes it possible to proceed with the genetic analysis of differences in row number. It demonstrates, however, the futility of attempting to study the genetics of row number as such. We must instead consider the genetics of condensation *and* whorl number *and* multiplication. Genetic investigations along these lines are already under way. The results now available, though not precise, suggest the general nature of the genetic background. Condensation is apparently due to one or two recessive genes with a considerable number of factors modifying its expression. Differences in whorl number are apparently due to at least several genes; the problem is a complex one. In an 8-rowed variety or in a 12-rowed variety the correspondence between whorl numbers in the tassel and in the ear are absolute. In crosses between such varieties, thresholds of expression may differ in different parts of the tassel and between the tassel and the ear.

THE BEARING OF THESE EXPERIMENTS UPON THE GENETIC ANALYSIS OF MULTIPLE-FACTOR CHARACTERS

Few branches of genetics are of more practical or theoretical significance than those which deal with the inheritance of multiple-factor characters. Yet in this field of genetics little fundamental advance has been made since East first demonstrated that the problem could be brought in line with a single-factor analysis. Row number in maize is such a problem. As the above analysis shows it cannot be understood genetically until it is understood morphologically. Now that we understand something about the morphological and physiological apparatus by which increases in row number are achieved, we are ready to plan a genetic experiment in which the number and distribution of genes responsible for row number differences may be determined, at least approximately.

To work effectively in such problems, one must, in other words, precede genetic analysis with morphological analysis. In a problem of this complexity, the morphological analysis is in itself a subject for research. This is equally true in most other investigations of multiple-factor characters. The general neglect of the morphological bases of such characters is one of the reasons the subject has progressed so little in the last thirty years.

THE ANATOMICAL INTERPRETATION OF THE EAR AND TASSEL

The inflorescences of *Zea Mays* have proved notoriously difficult to explain in terms of classical morphology. Weatherwax (1935) has pointed out that they share with certain other grasses a tendency to be whorled rather than distichous. That does not, however, solve the fundamental difficulty in interpretation. Why should the lower branches of a maize tassel be distichous and the upper branches spiraled or whorled? The facts reported above suggest an explanation. If we confine our attention to non-teratological inflorescences, the typical tassel has distichously arranged branches at its base, then passes through a zone difficult to interpret exactly and has whorls of spikelet pairs all along its upper portion.

Furthermore, these whorls alternate in an exact fashion between two clearly opposite types. If the whorls are of two pairs, for instance, the arrangement is decussate. The distichous branches at the base and the alternation of oppositely arranged whorls at the apex suggest that the tassel is fundamentally distichous throughout and that in the upper part of the tassel each branch has been reduced to a whorl of two or three spikelet pairs as the case may be. The intermediate zone would then be the region in which the reduction of a tassel branch to a whorl of branches has been only partially accomplished.

One argument in favor of this interpretation is that the uppermost tassel branches, those just below the central spike, are themselves clearly whorled, usually for one node and sometimes for two or more. On the view expressed above each of these whorls of two or three branches would represent one branch with its own branchlets condensed upon the main axis, as illustrated in fig. 6. Whorls of two would represent a branch with one branchlet, whorls of three a branch with two. It is perhaps significant that the northern flint corns which are almost universally decussate in their central spikes are also characterized by lower branches which have but a single branchlet.

SUMMARY

1. The problem of row number in maize was studied in the tassel as well as in the ear, the former organ being more accessible for study and its variation being more readily interpreted.

2. One of the chief variables in maize is "condensation," a telescoping of successive internodes. It operates throughout the tassel and the ear but is most effectively measured in the lowermost secondary branch of the tassel. When precisely scored it is directly related to row number by the equation $C = 10\ R$. In United States maize this relationship is less exact above 20 rows, probably due to the intensive selection against varieties with more than that row number during the corn show era.

3. If we rule out those varieties of maize with condensation and multiplication as being teratological abnormalities, then all the remaining varieties have central spikes (and ears) with spikelets in whorls rather than in spirals as has been so frequently reported. Eight-rowed varieties such as the northern flints are in whorls of two; 12-rowed varieties are in whorls of three.

4. The genetics of row number is therefore most effectively studied not as the genetics of row number as such, but as the genetics of condensation, multiplication, and whorl number. Preliminary results indicate that condensation is a simple recessive and that the genetics of whorl number differences is complex.

5. Two problems are discussed in the light of these results: The genetics of multiple-factor characters, and the anatomical interpretation of the ear and tassel.

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THE VASCULAR ANATOMY OF THE FOUR-ROWED EAR OF CORN

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The question of row number eventually arises in any complete study of the ear of corn. It is likely to become involved especially when the origin of the ear is considered. Several years ago the late Dr. R. A. Emerson was growing certain strains of corn in a study of row inheritance. He obtained several ears with four rows from some of the crosses and these were made available to the writer for anatomical study. The immediate ancestry of the plants which produced these ears is not known.

METHODS AND MATERIALS

The same general methods were employed for the examination of the internal anatomy of these 4-rowed ears as were used for the 8-rowed ear.[1] The ears were studied when mature in size but sufficiently soft so that, without embedding and further treatment, serial sections of 160 μ could be made. No staining was necessary to distinguish the vascular bundles when sections were mounted in glycerin. In addition to cross-sections, retted material was used to aid in getting a three-dimensional picture.

The ears examined conformed in external appearance to descriptions which have already been given for this type of ear. The spikelets were arranged in two pairs of rows opposite each other (pl. 36, fig. 1), thus giving a rectangular appearance in cross-section. Between the pairs of rows were smooth faces. Had these been 8-rowed ears, pairs of rows would have formed on these faces. The specimens showed occasional extra kernels indicating the development of the second flowers of some spikelets.

The general pattern of description used is that previously employed for the 8-rowed ear to which frequent reference will be made. In order to distinguish the vascular bundles of the inner and outer systems in the diagrams more readily, those of the inner system have been partially blocked in.

DESCRIPTION

The change in number, the size, and the arrangement of the bundles in the transition region from the shank to the ear could not be made since the specimens had been collected without the shanks. All indications were that it was essentially like that of the 8-rowed ear previously discussed. The diagrams used in the description represent a part of a series of cross-sections cut about halfway up the ear and extending about four nodes (assuming that each pair of spikelets represents a node) acropetally. The staggering of the pairs of spikelets on the opposite sides aided in interpretation.

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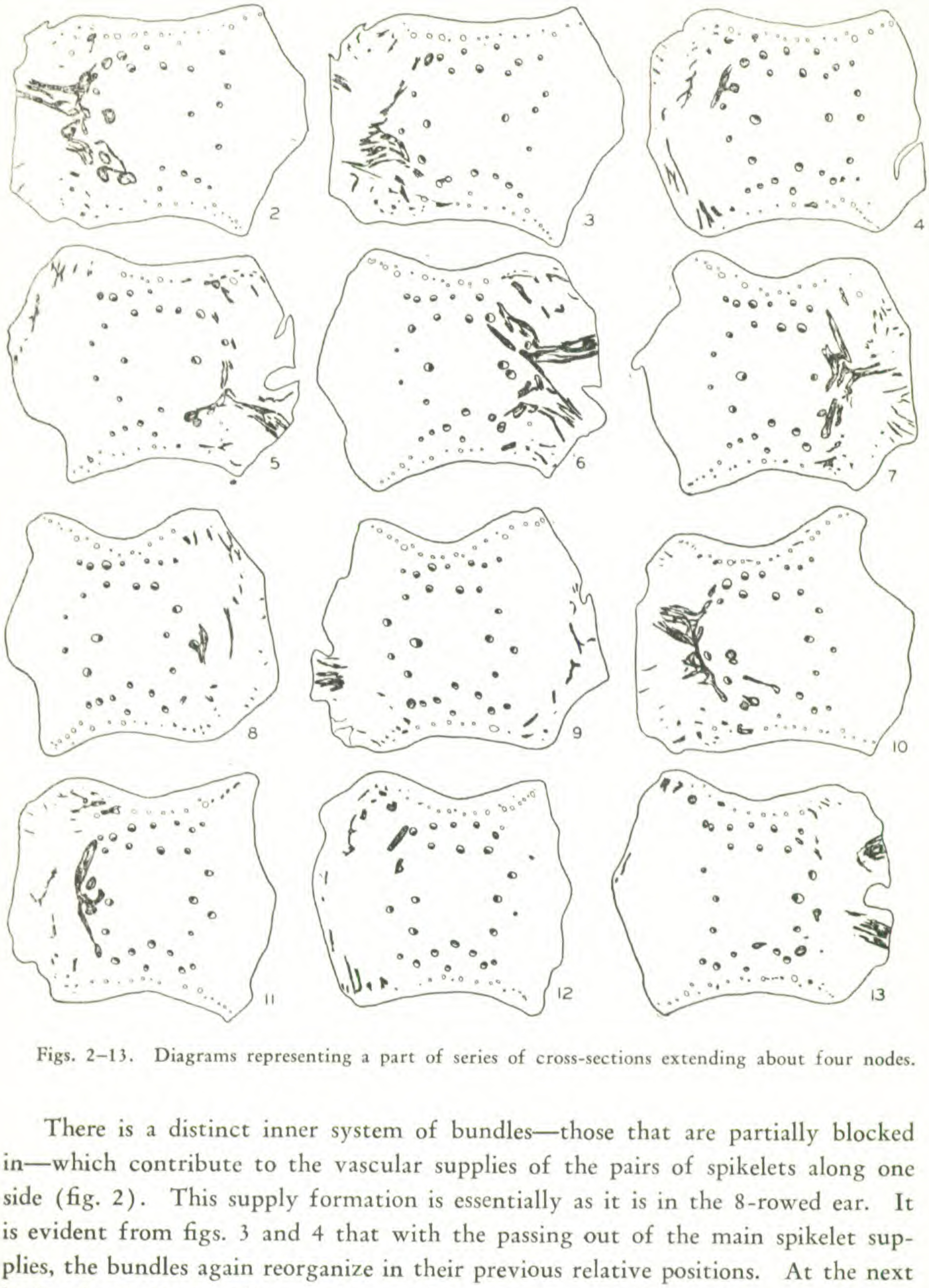
[1] Laubengayer, R. A. Paper in press.



Figs. 2–13. Diagrams representing a part of series of cross-sections extending about four nodes.

There is a distinct inner system of bundles—those that are partially blocked in—which contribute to the vascular supplies of the pairs of spikelets along one side (fig. 2). This supply formation is essentially as it is in the 8-rowed ear. It is evident from figs. 3 and 4 that with the passing out of the main spikelet supplies, the bundles again reorganize in their previous relative positions. At the next higher level, the bundle complex on the opposite side is forming the next higher spikelet supplies (fig. 5). This is obviously a repetition of the reorganization of the vascular system at the lower level. The inner system at the level of fig. 9 is shown in its entirety without any spikelet supplies. From the level indicated in

fig. 10 through that shown in fig. 11, the supplies to the next higher pairs are indicated. Thus, there is a very uniform sequence of vascular supply formation acropetally.

It is obvious that the bundle organization is much like that in the 8-rowed ear, as seen by the inner system at the level indicated in fig. 9. If the courses of the median bundles along the smooth faces are followed, it is seen that these are not involved in contribution to the spikelet supplies. This was found to be true in all ears studied except in a single small one. In this one, all bundles of the inner system contributed to the spikelet supplies. Bundles facing the smooth side also contribute in the formation of the spikelet supplies. Hence the system of vascular bundles contributing to the supply of the spikelets is far more extensive laterally than was evident in the 8-rowed ear.

The outer system of bundles is likewise more extensive than was observed to occur in the 8-rowed. As seen in all the figures, the bundles are arranged across the sides without spikelets, with a greater concentration at the corners which are directly associated with the supplies to the glumes (figs. 3–5 and 7–9). There is a lateral anastomosing of these same corner bundles between the levels at which the spikelet supplies leave the axis. This anastomosing gives complete continuity of the bundles of this outer system across the sides bearing spikelets.

A number of bundles of this outer system along the smooth side do not enter into the supplies to any parts. They run the entire length of the ear with little lateral fusion. Thus along the smooth face, there is at least one of the bundles of the inner system and a number of the outer system which run the length of the ear without supplying any organs.

As an aid in the interpretation of these systems, the retted material as shown in pl. 36, fig. 14 helps considerably. Not only do the vascular supplies to the glumes stand out in definite profile, but the remainder of the vascular bundles of the outer system show clearly across the smooth face. Bundles of the inner system can be seen plainly even though they lie below the outer.

DISCUSSION

The anatomical structure of the 4-rowed ear shows a striking similarity in structure with that of the 8-rowed. That there are present two distinct systems of vascular tissue cannot be emphasized too strongly. Paralleling the condition in the 8-rowed ear, the stronger inner system furnishes the main supplies to the paired spikelets. These supplies are formed over a very short distance vertically and pass out almost at right angles into the spikelet axes. In contrast to the condition present in the 8-rowed ear, the bundle complex involved in the supply to the spikelets is greater in circumference so that the total bundle supply is greater than in the 8-rowed. However, there are usually some bundles which do not enter into these supplies—those always on the sides that bear no spikelets. Only in one small ear examined were all the bundles associated with spikelet supplies.

The outer system is relatively stronger than that in the 8-rowed ear. At the margins of the faces which bear the spikelets, the smaller bundles behave in the same fashion as in the 8-rowed. They furnish the complete vascular supply to the two glumes of each spikelet, completely independent of the outer system. Between the levels at which the main supplies to the spikelets pass out, they form complete lateral connections. The presence of bundles of this system offers an unusual condition on the two sides along which there are no spikelets. These bundles show very little lateral fusion and extend the entire length of the ear. They were in no way connected with the supply to any structure in the specimens studied.

The presence, along the two smooth sides of the ear, of parts of the inner system and outer system is significant. From a physiological standpoint, there is far greater proportion of vascular tissue present than would usually be present to supply such an amount of tissue. It is generally accepted that in all groups of plants there are forms which show relatively large amounts of vascular tissue supplying comparatively small masses of tissue. This is usually interpreted as evidence of reduction; the loss of an organ or organs often is completed before the disappearance or radical modification of the vascular tissue supplying these organs. The vascular tissue represents a conservative portion of the plant body and therefore responds more slowly to change in conditions. If this is true in the case of the 4-rowed corn ears, then the present 4-rowed condition is a derived one. Hence it would not represent a primitive condition—if one uses the number of paired rows as a criterion—but a more advanced one; a simpler condition derived from a more complex one. This would be in keeping with the interpretation of similar structures found in other plants. If this is true in the 4-rowed ears, it may be that similar reductions may exist in the higher-rowed ears, with internal evidence. This might well necessitate a general change in the interpretation of the row number of the corn ear.

SUMMARY

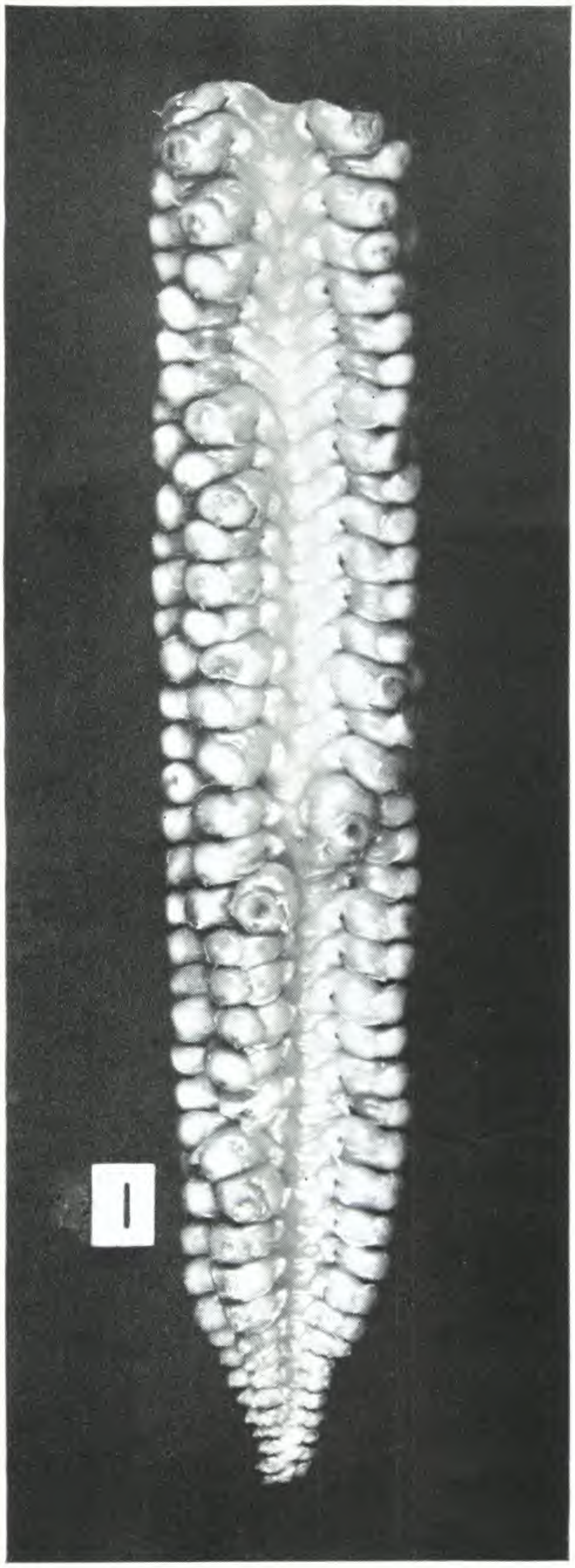
The 4-rowed ear of corn shows a basic pattern of vascular tissue which resembles that of the 8-rowed ear. There exist pronounced inner and outer systems which probably differentiate at the base of the ear. The inner system furnishes the main vascular supply to the spikelets; the source of supply is more extensive circumferentially than in the 8-rowed ear. The outer system is associated with the supplies to the lower glumes. The presence of bundles of the inner and outer systems, which do not supply any organ, along the sides without spikelets indicates that a reduction has occurred.

Explanation of Plate

PLATE 36

Fig. 1. Side view of four-rowed ear of corn.

Fig. 14. Retted specimen of four-rowed ear.



LAUBENGAYER—ANATOMY OF FOUR-ROWED EAR

GENERAL FEATURES OF THE EPIDERMIS IN ZEA MAYS[1]

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I. TECHNIQUES FOR STUDYING THE EPIDERMIS OF CEREALS AND GRASSES

In the plant kingdom the epidermis reaches its highest degree of differentiation in the Gramineae. Therefore it displays in this group a rich choice of specific characters which can be used in the genetic study of cereals as well as in the general taxonomy of the family (Prat, 1932). To obtain valuable results in this field it is necessary to make a careful examination of the epidermis on all the parts of the plant, by using a wide range of techniques and enlargements.

A. *Direct examination.*—

First, all the leaves and internodes from the base to the summit of the culm, as well as the floral bracts, must be examined with a dissecting binocular. All the features of the epidermis should be noticed, and at this stage of the work a preliminary distribution map of the most conspicuous elements can be drawn. However, this direct examination is never sufficient, some categories of cells requiring higher magnifications than others; hence the necessity of making cross-sections and peels.

B. *Peels.*—

The shortest way to obtain preparations of the epidermis is to peel off portions with forceps. However, this is possible only in the most favorable cases, while the technique of scraping described below serves under almost all conditions.

C. *Scraping.*—

Place on a glass slide the part to be studied: leaf, internode, etc., *the epidermis which is to be examined being face down.* Scrape away carefully with a scalpel all the overlying tissues, removing everything except the epidermis in question. Then turn the piece of epidermis upside down for microscopic examination. This operation is, in general, easy and rapid with fresh tissues. Dry material as, for instance, herbarium specimens, may be put in a softening medium of equal parts of glycerin, alcohol and water, for two or three days before dissection.

D. *Staining.*—

The pieces of epidermis can be observed immediately under the microscope. For a more detailed study of the cell walls the best technique is a double staining, using methylene blue and ruthenium red: (1) Put the tissue in a solution of

[1]This article is a part of a wider investigation on epidermic characters of maize. Travel expenses were covered partly by the Missouri Botanical Garden, partly by a fellowship of the John Simon Guggenheim Foundation; material was provided by the experimental fields of California Institute of Technology, Missouri Botanical Garden, Pioneer Hi-Bred Corn Co., Harvard University, and Montreal Botanic Garden. I express my heartfelt thanks to Drs. George T. Moore, H. A. Moe, E. G. Anderson, Edgar Anderson, William L. Brown, P. C. Mangelsdorf, J. Rousseau, and H. Teuscher, for the help so kindly given.

methylene blue and alum for one-half minute; (2) wash it thoroughly; (3) place it in a watch glass in distilled water; then add a small quantity (less than a pin-head) of the powder of ruthenium red (solutions of this substance in water being unstable, it is necessary to prepare immediately at the time of use); let it remain for half an hour.

Cellulose cell walls will be colored a bright red, the intensity of color being chiefly in proportion to their content of pectic substances; sclerified cell walls will appear blue, suberous ones green. The progress of the ruthenium staining can be watched under the microscope until the desired intensity is reached. The preparation is then dehydrated rapidly in alcohol (70, 90, 100 per cent), put in xylol, and mounted in Canada balsam. Such slides can be kept indefinitely, though they decolorize slowly after some years. If ruthenium red, a rare and expensive substance, cannot be obtained, double staining by iodine green and alum carmine may be used successfully, though giving less brilliant colors.

E. *Observation.*—

The entire range of microscopic enlargements is useful for a study of the epidermis, from the lowest objectives for observing the general distribution of elements, up to immersion objectives for the tiniest cell details. All the resources of the condenser and of the diaphragm are needed to sharpen the contrasts between the elements and to accentuate their relief. For observing silica cells, hydrating mediums such as chloral lactophenol are useful in order to increase the difference in refraction indices between silica and neighboring tissues and to render those cells more conspicuous.

F. *Cross-sections.*—

Epidermic preparations obtained by peeling or scraping show the shape of the cells in vertical projection only. To recognize their other aspects it is necessary to examine also cross-sections of the whole organ, leaf or internode, both in transverse and longitudinal planes. These sections enable us also to observe the anatomical connections of epidermis cells with subjacent tissues. The best technique for staining them is again methylene blue and ruthenium red. After a careful microscopic examination of all epidermis preparations and cross-sections it is always necessary to examine again, in their living state, the entire organs of the plant with the dissecting binocular, in order to map the distribution of the elements precisely.

II. CATEGORIES OF ELEMENTS IN GRASS EPIDERMIS

Epidermis cells are regularly disposed in straight rows over almost the entire body surface of a grass. Some of them are elongated in the same direction as the organ on which they are borne (internode, leaf or bract), while others remain short; hence the classical distinction between "long cells" and "short cells." It is really better to distinguish "fundamental elements"—generally but not always elongated—and "differentiated elements."

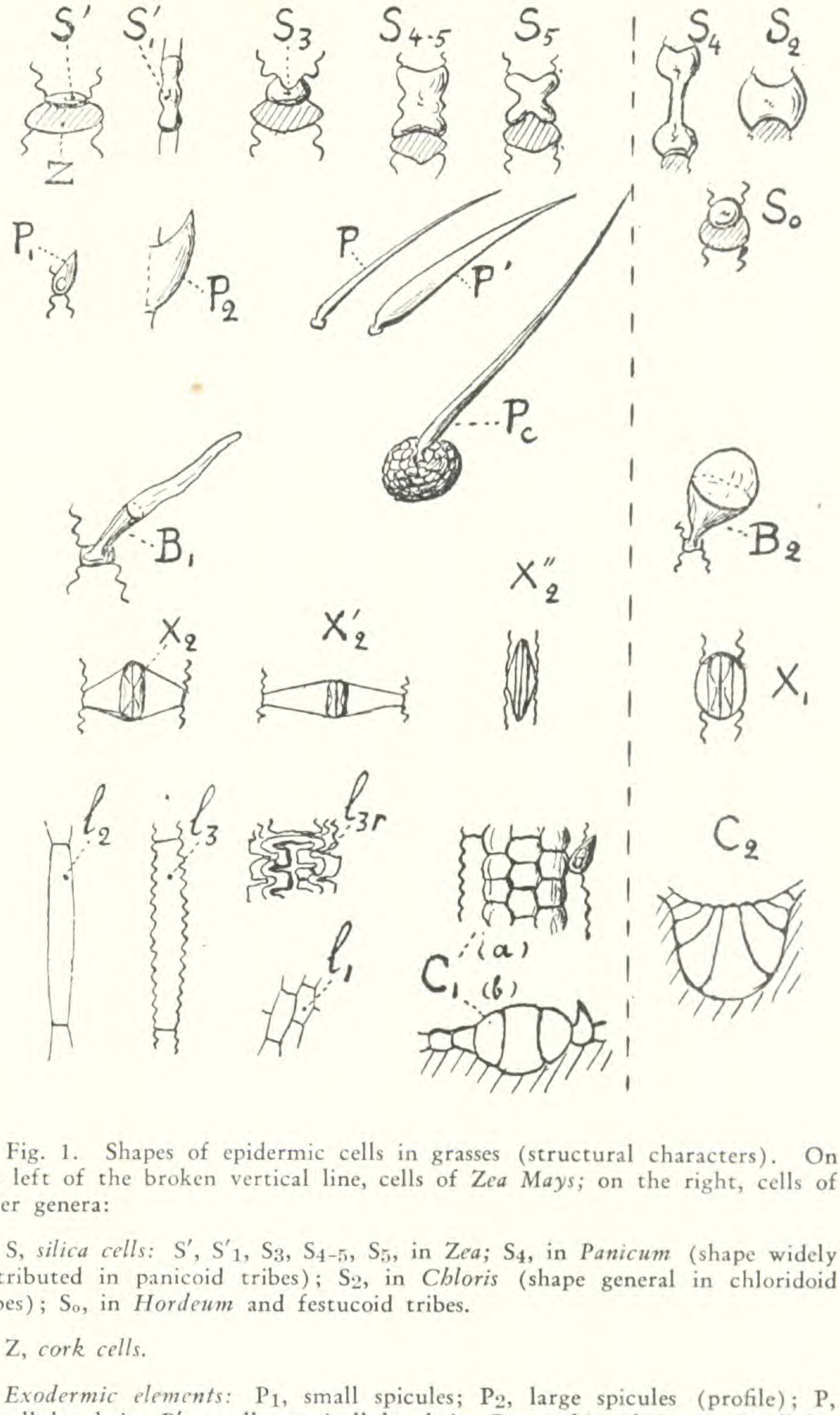


Fig. 1. Shapes of epidermic cells in grasses (structural characters). On the left of the broken vertical line, cells of *Zea Mays;* on the right, cells of other genera:

S, *silica cells:* S', S'_1, S_3, S_{4-5}, S_5, in *Zea;* S_4, in *Panicum* (shape widely distributed in panicoid tribes); S_2, in *Chloris* (shape general in chloridoid tribes); S_o, in *Hordeum* and festucoid tribes.

Z, *cork cells.*

Exodermic elements: P_1, small spicules; P_2, large spicules (profile); P, unicellular hair; P', swollen unicellular hair; P_c, cushion hair; B, bicellular hair; B_1, eu-panicoid shape; B_2, chloridoid shape.

X, *stomata:* X_2, lozengic shape present in *Zea,* with variants; X'_2, X''_2, X_1, ovoid shape (*Hordeum*).

l, *fundamental cells:* l_2, with straight walls; l_3, with undulated walls; l_{3r}, with thick and undulated walls; l_1, remaining short in transition zones.

C, *bulliform cells:* C_1, in *Zea* (a), vertical projection, (b) transverse section; C_2, in *Panicum* (transverse section).

It is worth noticing that only the first of these categories of cells is sensitive to auxins. At a given growth stage the length of a "long cell" in the meristematic base of an internode or of a leaf can be increased suddenly 200-fold in a lapse of several hours. During the same time the length of the adjacent "short cells" is only slightly modified. The body of these cells seems to escape the influence of growth hormones, probably on account of their precocious senescence; hence their shape is more constant and more interesting for displaying specific characters.

A. *Differentiated elements.*—

The differentiated elements fall into four great categories: (1) silica cells; (2) exodermic elements; (3) cork cells; (4) stomata.

1. The *silica cells* are precociously filled with a jelly of colloidal silica, which becomes a solid transparent block as the protoplasm dies. They may take the shape of halters, crosses, battle-axes, half-moons, etc., or be simply round or rod-shaped (fig. 1, S), these shapes being characteristic of sub-families and tribes of the Gramineae.

2. The *exodermic elements* include the differentiated cells or groups of cells which extend above the common level of the epidermis. Most of these are formed by a single cell: (1) *Unicellular hairs* (fig. 1, *P*); (2) Small or big *spicules* (P_1, P_2), which are present in all groups of the family. Others are formed by two or many cells, and they exist only in definite tribes: (3) *Bicellular hairs* (fig. 1, *B*), made up of two cells of different textures. The walls of the basal cell are strong and sclerified, those of the distal one, thin and cellulosic, giving an interesting example of unequal segregation of potentialities in the division of the mother cell; (4) *Cushion hairs* (fig. 1, *Pc*) consisting of big hairs formed by one cell but each arising in the middle of a hemispheric protuberance formed by a large number (20 or more) of small differentiated cells.

3. The *cork cells* (or suberous cells) (fig. 1, Z) do not by themselves exhibit characteristic shapes but are molded by neighboring elements. Their protoplasm dies early, being surrounded by impermeable walls of suberin. They offer an interesting case of cell polarity. When the mother cell of a differentiated cellular group divides, if a cork cell is produced it is always situated on the basal side of the group, i. e., toward the base of the organ. The other element, silicous or exodermic cell, is always apical.

4. The *stomata* (fig. 1, X) are formed by four cells, a special feature of the Gramineae, instead of two as is usual in other families. Their shape can be ovoid (X_1) or lozengic (X_2). Their distribution is interesting from the anatomical point of view on account of their connection with chlorenchyma, and from the ecological one. For example, in xerophytic species stomata are often absent on the outer face of the blade and localized on the inner face, being therefore enclosed in the leaf when it shrinks and rolls up into a tube during dry periods.

B. *Fundamental elements.*—

The fundamental cells always constitute the greatest part of the epidermic area. However, they are less interesting than the differentiated ones, their shapes being more uniform and exhibiting barely conspicuous specific characters. Their walls may be straight (fig. 1, l_2) or undulated in connection with small punctiform depressions in the outer wall (l_3). On strengthened regions these walls may become thick and deeply furrowed (l_{3r}). In certain species the outer wall may bear cuticular warts or hollow papillae. Cells of this category are generally much elongated. Their length may reach up to 300 times their width, but they may also, in certain areas, remain short, almost square (fig. 1, l), as in transition zones (nodes, sheath bases, blade bases). This is why the term of "long cells," usually applied to them, is a misnomer.

C. *Bulliform elements.*—

On the leaves of certain genera, chiefly on the inner face of the blade, regular stripes can be observed, consisting of "bulliform" cells. They are aquiferous, strongly turgescent cells, sometimes reaching a great volume by expanding perpendicular to the leaf surface (fig. 1, C_2). In vertical projection they are shorter than the neighboring fundamental cells (fig. 1, C_1a). They may be considered as a separate category, distinct from both fundamental and differentiated elements. By losing their water in dry air they function in the rolling of the leaf in some xerophytic species, hence the name "motor cells" which is sometimes applied to them.

III. DISTINCTIONS OF THE SUBFAMILIES OF GRASSES ACCORDING TO THEIR STRUCTURAL EPIDERMIC CHARACTERS

A. *Structural characters.*—

For an efficient utilization of epidermic features in taxonomy or genetics it is necessary, first, to recognize the respective values of all the characters which may be distinguished and to determine their order of subordination (Prat, 1933, 1936). Up to now we have referred only to the shapes of the epidermis cells and mentioned that they may differ from one group to another. In this way we find a first category—the *structural* characters. They are characters of the *first order,* i. e., they can be applied to distinguish the great subdivisions of the family: sub-families and tribes.

The first step in analyzing the epidermis of a Grass will be thus to determine *what shapes of cells are present.* In general, this is sufficient to reveal the subfamily, the tribe, sometimes the genus, and we can obtain this information on a tiny fragment of leaf some square millimeters in area; hence the importance of the method in certain practical researches, for instance, in tracing the origin of certain manufactured products.

B. *Subfamilies.*—

The subfamilies Bambusoideae and Panicoideae possess the most complicated shapes of silica cells (fig. 1, S_4, S_5) in the eu-panicoid tribes, (S_2) in the chloridoid ones. In the subfamily Festucoideae only the simplest types of silica cells (S, S_1) are present. In Bambusoideae and Panicoideae also there are bicellular hairs, threadlike (B_1) in the eu-panicoid tribes, and swollen (B_2) in the chloridoid. The cushion hairs (P_c), too, are correlated with the Panicoideae subfamily. The true Festucoideae never possess either bicellular or cushion hairs (Prat, 1936).

Thus we may distinguish the structural epidermic characters of the great subdivisions of the Grass family:

(1) Bambusoideae, primitive group including arborescent forms, with the most complex epidermis.

(2) Panicoideae, mostly a herbaceous group retaining complex shapes of epidermic cells but with a specialization appearing in two directions:

(a) *Eu-panicoid type* characterized by halter-shaped silica cells (S_4), threadlike bicellular hairs (B_1). Includes the tribes Paniceae, Andropogoneae, Maydeae.

(b) *Chloridoid type* characterized by silica cells molded in the shape of battle-axes with double edges (S_2) and by swollen bicellular hairs (B_2). Includes the tribes Chlorideae, Eragrosteae, Sporoboleae.

(3) *Festucoideae,* herbaceous subfamily showing a marked simplification of the epidermic cell shapes, absence of bicellular and cushion hairs, and only the simplest shapes of silica cells (S, S_1). This group includes the tribes Festuceae, Hordeae, Aveneae, Agrostideae.

These structural differences in the epidermis between the subfamilies are in perfect harmony with equally important anatomical and cytological differences which distinguish the same groups; for instance, the radial disposition of the chlorenchyma around the vascular bundles in the leaves of Panicoideae, but not in Festucoideae; the basic number of chromosomes, 7 in Festucoideae, 5 or 9 in Panicoideae (Hunter, 1934); the first green leaf of the seedling, narrow and vertical in Festucoideae, broad and extroverted in Panicoideae, etc. The geographic distributions, too, are different: Bambusoideae and most of the Panicoideae are localized in tropical regions; Festucoideae in temperate and cold countries.

The concordance between these diverse categories of characters—epidermic, anatomical, cytological, etc.—gives a practical basis for revising the systematics of the Gramineae in order to reach a more natural classification showing the real affinities of the genera (Prat, 1936), the present classifications still being artificial and inadequate in many parts.

IV. STRUCTURAL CHARACTERS OF THE EPIDERMIS OF *ZEA MAYS*

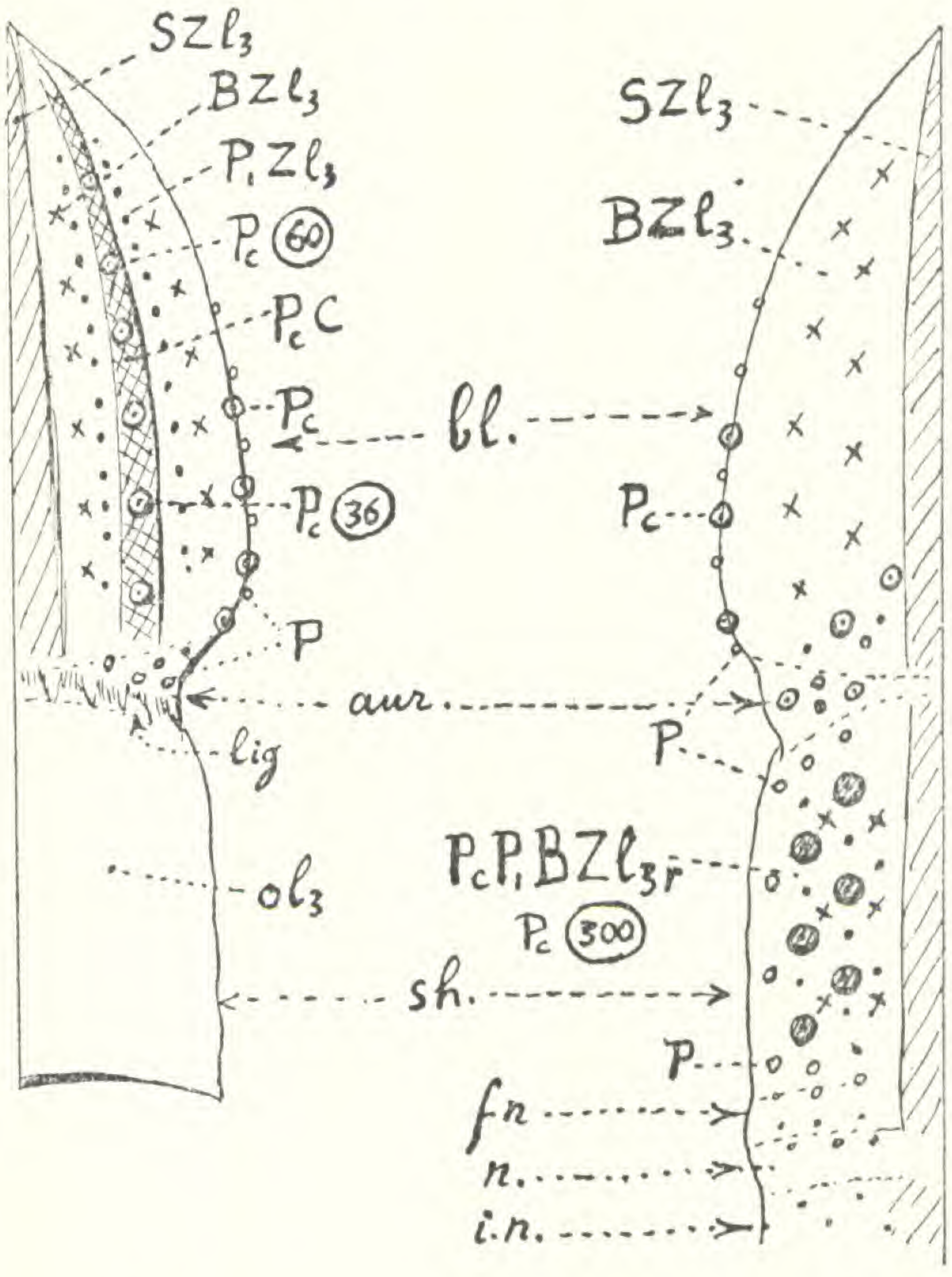
A. *Shapes of cells.*—

On the leaves of maize we found the following categories of epidermic cells (see fig. 1, left side):

(1)—silica cells of the types: S', S'_1, S_3, S_{4-5}, S_5.
(2)—small and big spicules: P_1, P_2.
(3)—thread-like bicellular hairs, B_1.
(4)—cushion hairs, P_c.
(5)—cork cells, Z.
(6)—quadricellular lozengic stomata, X_2.
(7)—fundamental cells, mostly with undulated walls, l_3, and also, on localized areas, the types l_{3r}, l_2 and l_1.
(8)—bulliform cells of the type C_1.

B. *Taxonomic position of Zea Mays.*—

This epidermic structure belongs strictly to the eu-panicoid type and agrees with the anatomical and morphological characters in placing the genus *Zea* in the subfamily Panicoideae, near the eu-panicoid tribes Andropogoneae and Paniceae. The recognized affinities of the Maydeae with the Andropogoneae are thus confirmed by the structural epidermic characters.



I II

Fig. 2. Dermogram of the upper leaf, Mexican dent corn No. 1061 (distributive characters):

I, inner face of the leaf; II, outer face.

bl, blade; aur, auricular triangle; lig, ligula; sh, sheath; fn, false node; n, node; i.n., internode.

Letters representing the epidermic cells are the same as in fig. 1. Cushion hairs are figured by dots in circles (hatched when the cushion is colored red), ordinary hairs by circles, spicules (P_1) by dots, bicellular hairs (B) by crosses, bulliform stripes by cross-hatching, dense silica cells by hatching. Numbers in circles show the average density of cushion hairs per square centimeter.

V. DISTRIBUTIVE CHARACTERS; DERMOGRAMS OF CORN LEAVES

A. *Characters based on the distribution of epidermic cells.*—

The structural characters are not the only ones to consider in the epidermis of a Grass. The distribution of the different types of cells on all the organs of the plant (leaves, internodes, glumes, etc.) obeys precise rules and shows notable differences from one species to another, and within a species from one variety to another. The *distributive characters* thus constitute a second category of taxonomic importance. They are less fundamental but allow more delicate distinctions than the structural ones, as they provide a means of distinguishing smaller groups (species or varieties) instead of subfamilies and tribes. For this reason they are the most valuable for taxonomic or genetic work.

B. *Conception of dermograms.*—

The distributive characters can be shown in "dermograms," schematic maps figuring the position of the principal categories of epidermic cells. Figures 2 and 3 show examples of leaf dermograms for two varieties of Maize. The leaf represented must preferably be the upper one, just below the tassel, for this leaf displays to the utmost the specific characters. The leaves at the base of the culm are less differentiated, this fact being connected with the general law of histological gradation (Prat, 1934, 1945).

In figs. 2 and 3 only one-half of the leaf is represented, inner and outer face, and on this only one vein. The complete representation of all the veins with all their epidermic cover would give an infinitely complicated and useless diagram. For the need of simplification also, only the elements of interest for systematic comparisons are figured. For instance, stomata are not indicated on the scheme, their distributions being about the same in the varieties under comparison.

According to their size, spicules are figured by small or big dots (P_1 or P_2), unicellular hairs (P) by circles, bicellular hairs (B) by crosses, cushion hairs (P_c), by dots in circles. Regions where the differentiated elements are absent or consist only of stomata are left in white (ol); bulliform stripes (C) are represented by cross-hatching; regions with abundant silica cells (S) by hatching.

The precision of the dermogram can be increased by indicating the density of the most characteristic elements on different regions of the leaf. This density is easy to calculate by counting these elements in the field of a dissecting binocular for the biggest ones, such as cushion hairs, or in the field of a microscope for the smallest, such as bicellular hairs, and reducing to the unity of surface. On fig. 2 the numbers inscribed in circles indicate the local density of cushion hairs (P_c) per square centimeter.

C. *First example: Mexican Dent No. 1061.*—

The first example (fig. 2) is a small-seeded Mexican dent corn from El Capulin, bearing the number 1061 in the experimental cultures of Dr. E. G. Anderson, California Institute of Technology. The most striking feature of this

variety is the abundance of cushion hairs (P_c) on the entire outer face of the sheath (base of diagram II, fig. 2). Their density reaches here an average of 300 per square centimeter. On this area the cushion cells are colored a strong purple by an anthocyanin contained in their vacuole, and those cushions are conspicuous to the naked eye as small red dots. The hair itself is white, appearing under the microscope as a giant column with a constricted base, arising in the middle of the protuberance formed by the colored heap of dwarf cushion cells. The contrast between white hairs, purple cushions, and green surrounding tissues (chlorenchyma appearing through the uncolored flat epidermis) is striking when observed with the dissecting binocular, the more so as the cushion protuberances are strongly marked in this variety. The purple tint of the cushions appears only on the portions of sheaths exposed to the light.

On the outer face of the sheath the density of cushion hairs can reach up to 300 per square centimeter. We may notice also on the outer face small spicules (P_1), bicellular hairs (B), cork cells (Z) and, chiefly on the veins, silica cells (S). The fundamental cells present strongly undulated and thickened walls (l_{3r}). The inner face of the sheath (base of I, fig. 2) is covered by the simplest type of epidermis—only thin-walled fundamental cells (l_3) with few stomata.

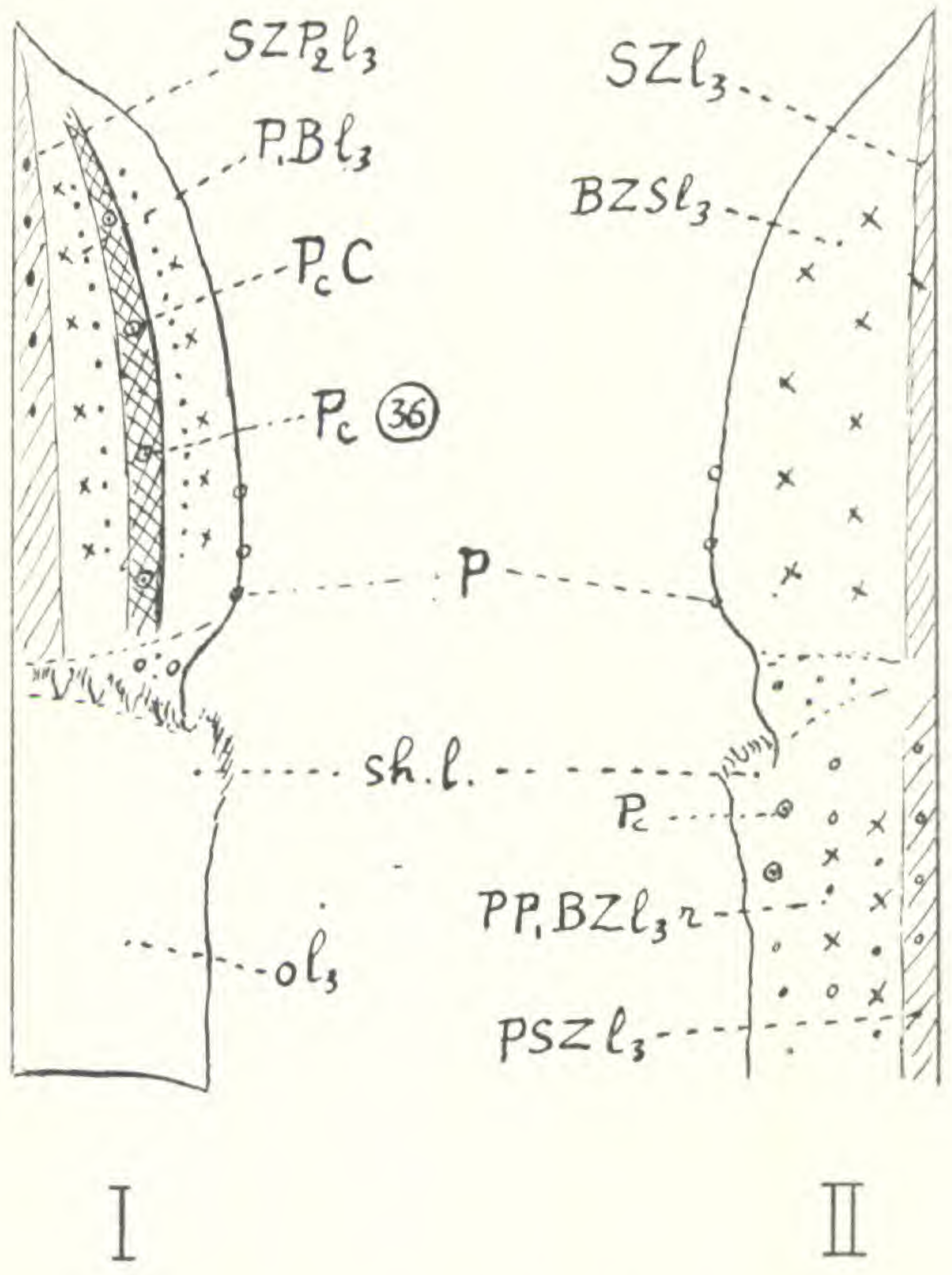


Fig. 3. Dermogram of the upper leaf, inbred yellow dent corn L317 (distributive characters):

Sh. l, sheath lobes; other conventions same as in fig. 2.

The inner face of the blade (summit of I, fig. 2) offers as its most striking feature conspicuous stripes of bulliform cells (C) located between the veins. On these stripes we observe from place to place big cushion hairs (P_c) analogous to those of the sheath, with the difference that their cushion is not colored purple though it is exposed to the light. On each side of a bulliform stripe is a dense row of small spicules (P_1). In addition, the inner face of the blade shows bicellular hairs (B_1), cork cells (Z), and chiefly on the ribs, silica cells (S). The fundamental cells (l_3) have undulated walls of medium thickness. In this variety the density of cushion hairs is lower on the inner face of the blade than on the outer face of the sheath; it can vary from 36 per square centimeter at the base of the blade up to 60 at the summit.

On the outer face of the blade (summit of II, fig. 2) we find no bulliform stripes, and only very rarely cushion hairs, localized at the base of the blade, mainly on the edges and on the auricular triangle. The exodermic elements are represented chiefly by bicellular hairs, spicules being scarce. The difference between the two faces of the blade can be recognized simply by feeling them with the finger tip, the inner face being minutely scabrous on account of its numerous small spicules (P_1), the outer face perfectly smooth to the touch. The bicellular hairs are too small and too soft to be perceptible.

D. *Second example: Inbred Yellow Dent No. L317.*—

Our second example is a yellow dent corn inbred, widely used in the United States corn belt, L317 (Cal. Tech. experimental field, Arcadia, summer 1948). The dermogram of this variety (fig. 3) differs from the preceding one chiefly by the outer face of the sheath (base of II). There the cushion hairs are very scarce and localized near the sheath lobes (these lobes are here much more developed than in the previous example). The cushion of these hairs is small, feebly protuberant, and not colored purple. The elements noticeable on the outer face of the sheath are ordinary hairs (P), spicules (P_1), bicellular hairs (B), cork and silica cells, the latter chiefly on the veins. The fundamental cells have thick, undulated walls (l_{3r}).

The inner face of the blade (summit of I, fig. 3) also shows some differences from the first example. Numerous big spicules (P_2) are borne on the principal ribs; on the bulliform stripes (C) cushion hairs are present, with an average density of 36 per square centimeter, but their cushion is very small compared to those of the first variety. On the outer face of the blade (summit of II, fig. 3) the cushion hairs are absent, but ordinary unicellular hairs can be noticed on the edges and on the auricular triangle. Bicellular hairs are present on the stripes between the veins, silica cells chiefly on the veins, and cork cells on both.

CONCLUSION

We have demonstrated for maize how it is possible to describe epidermic characters of cereals in order to use them in genetic and taxonomic studies.

1. When studying the epidermis of a cereal or a grass, the first step is to recognize its *structural characters*, i. e., the nature and the shape of its component cells. The shape of the silica cells (S), the presence and the shape of bicellular hairs (*B*), of cushion hairs (P_c), of bulliform cells (*C*), etc., must be specially investigated (see fig. 1). These structural characters give immediately the means to determine the general systematic position of the plant, i. e., the subfamily, tribe, to which it belongs. Each genus has a definite set of epidermis cells with well-defined shapes, as one of its fundamental characters. In all the species of a genus we find the same types of cells with exactly the same shapes, but they are differently distributed from one species to another.

2. The second stage of the study is therefore to determine how these categories of cells are distributed on the leaves and on the floral bracts. We thus obtain a second category of characters: the *distributive characters*, which may enable us to identify the species. This distribution of epidermic elements can be expressed in schematic maps or "*dermograms*" (fig. 2). The "*dermotype*" of a plant, the sum of its epidermic characters, will be thus expressed: (1) by a detailed drawing of each category of cells forming its epidermis (fig. 1), showing the structural characters and defining the general systematic position of the genus (subfamily, tribe); (2) by a *dermogram* (figs. 2 and 3) indicating the distribution of each type of cells on the outer and on the inner face of the leaf (the upper leaf being more characteristic, is preferably chosen), of the glume, lemma and palea. These dermograms show the distributive characters and give a means for typifying the species and varieties.

An interesting development in the genetic study of maize will be to identify the genes controlling the transmission of distributive epidermic characters, to analyze their linkage with other characters, and to find their positions in the chromosomes.

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COMPARATIVE HISTOLOGY OF THE FEMALE INFLORESCENCE OF *ZEA MAYS* L.[1]

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INTRODUCTION

While an interest in the corn cob has been shown by those who have attempted to explain the origin and nature of the ear, the increasing role which the cob is assuming today in industry, in archaeology, and in studies of the origin of maize makes it imperative that a careful comparative study of the cob be undertaken.

For many years corn cobs played no special role in the economy of corn production since approximately 90 per cent of the corn produced in the United States was used on the farms for feeding of livestock and most of it was fed as unshelled ears. The cobs remaining from ears that were shelled for poultry feed and the like were often used for fuel. However, with the advent of hybrid corn and large seed-processing plants, cobs have become a major by-product of a rapidly expanding agricultural industry and today ways and means are being sought for their utilization. Of the various uses suggested, one of the most promising is that of a filler in commercially processed feeds. There is some experimental evidence on the feeding value of ground cobs (Gerlaugh and Rogers, 1936), and further experiments are now under way. Other possibilities include its use in the production of furfural or as a substitute for peat-moss.

The corn cob plays an even more important role in the hybrid seed-corn industry. Since the grains of corn are produced on the cob, the physical characteristics of that structure affect the handling of the ear during processing. It is known, for instance, that certain corns are more difficult to shell than others, some shatter easily, and in some the grains are removed with difficulty. Some cobs are soft while others are hard and tough; certain cobs are very susceptible to ear-rotting fungi, while others are rarely attacked by these oganisms. Since these differences are of considerable importance to the practical corn-breeder it is necessary that the anatomical, histological, and chemical reasons for these differences be understood.

There is another reason why a comparative study of the maize cob is desirable. Both in North and South America archaeologists have excavated a large number of prehistoric sites and have found maize remains in many of these excavations. A few of the best finds have yielded remarkably well-preserved ears, without even a kernel missing, although the ear may have been stored for many centuries. However, at least 90 per cent of the material in archaeological collections is cobs. Since the mature cob is a hard and durable structure and not particularly attrac-

[1]Part of an investigation carried out in the graduate laboratory of the Henry Shaw School of Botany of Washington University and submitted as a thesis in partial fulfilment of the requirements for the degree of Doctor of Philosophy. The investigation was made possible by a special fellowship from the Pioneer Hi-Bred Corn Co., of Des Moines, Iowa.

tive to insects and rodents, it will remain relatively unchanged in trash heaps for long periods of time if kept dry, and many of the richest finds have been made in extremely dry areas. In more humid areas often the only plant material found consists of carbonized cobs and in such areas the cob assumes an even more important role than it does in dry areas. Through a study of the surface features of the prehistoric cobs certain facts about the corn can be arrived at, as, for example, the general shape and size of the ear. However, an entirely new set of characters which are present in the cob must be utilized if we are to make the greatest use of the vast quantities of material collected by the archaeologists. Before we can do this it is necessary to know which characters vary and the extent of their variation, and this can only be determined by making careful comparative studies of the anatomical and histological features of the cobs of various kinds of maize.

There is a fourth reason why a comparative study of the female inflorescences of maize is needed, and that is for a study of the origin of maize. One of the best approaches to a study of the phylogeny of most groups of plants is through comparison of the reproductive structures of that group. This is especially true in the Gramineae where the vegetative structures are of less importance than in certain other families. Today there is as great a mass of literature concerning the origin of maize as for any other crop plant, yet there has never been a thorough comparative study of the anatomical and histological features of its female inflorescence. Before a basic understanding of maize can be reached such a study must be made, not only of maize but also of its close relatives. The present investigation is a beginning along such lines and is an attempt to determine which are the variable features in the cob and the extent of their variability in different kinds of maize.

REVIEW OF LITERATURE

The origin and nature of the ear of *Zea Mays* L. have been subjects for speculation since Indian corn was first described and many hypotheses have been presented to account for it. Finan (1948) has made a critical survey of the descriptions of corn as found in the literature of the early Spanish explorations and in the great herbals. Because the ear of maize was a structure different from anything with which they were familiar the early herbalists devoted considerable attention to that structure and apparently the earliest-known European illustration of the plant is a detailed drawing of a mature ear.

Although the ear of maize has been known and discussed in literature over such a long period there is no part of the corn plant about which there is such a paucity of anatomical information as the mature cob. On the whole, the investigators who have written most about the ear, aside from those describing varieties of corn, have been primarily concerned with its origin and with the homologies between the ear and the tassel. The literature on the subject has become voluminous. The reader is referred to Mangelsdorf's (1945) recent paper in which he discusses (pp. 33–73) the major hypotheses concerning the origin of the ear.

The principal reason for the lack of information about the anatomy of the cob is that it is a difficult structure to study in its mature state. A cursory examination of the cross-section of an ordinary corn cob discloses that it consists of very different types of tissue. The center of the cob contains large soft-pith parenchyma cells surrounded by a layer of stone cells of varying thickness which are often compacted to form tissue as hard as that found in the shell of a hickory nut. Interspersed in these two such different tissues is the tough-branched network of the vascular system. Weatherwax (1935) summed up the difficulties of studying the cob when he said:

> "Long before maturity, however, the development of a tough schlerenchyma in the peripheral vascular region of the rachis makes it difficult to secure instructive sections even when the technique applicable to woody tissues is employed."

Not only is the cob hard and tough but it is composed of hard and soft tissues together, and if it is held firmly enough to make it possible to cut the hard parts the soft parts are apt to be crushed or broken.

While the anatomical features of the cob have not been well understood, the gross morphological features of the ear have been discussed by numerous investigators, especially in so far as those features could be used in describing corn varieties. John Lorain (1825) in his 'Nature and Reason Harmonized in the practice of Husbandry' described the varieties of corn grown in eastern United States in his time. It is evident from his book that he had a rather clear understanding not only of the basic types of corn grown in that region but even the effects brought about by the mixing of the different varieties. Bonafous, in 1836, monographed *Zea Mays,* describing the varieties of corn known to him, and in 1866 Enfield described a number of varieties. Sturtevant (1899) published the most comprehensive work on the classification of corn varieties that had appeared up to that time and which with only minor changes has been used until recently. Anderson and his collaborators (1942, 1946) have shown the need for a new classification of the races of corn which would incorporate all evidence available, especially the evidence from archaeology and genetics. Such a classification must be a goal toward which to work.

Most of the early authors, in their descriptions of corn, mention the cob and often remark about its strange character as, for example, Vasey (1884), when he wrote, "female spikes (originally by monstrous or teratological development?) are grown together into a spongy, continuous club-shaped body, the 'cob'." None of the early workers made comparative studies of the surface features of the cob. As Mangelsdorf (1945) has written, "though not easily interpreted [the ear] is not difficult to describe," and he describes it as "a spike upon whose thickened axis (the cob) naked grains (caryopses) are borne in longitudinal or somewhat spiral rows: eight, ten, twelve or more in number." Weatherwax (1935) gives a somewhat similar description, writing of it as "being made up of a cylindrical 'cob' around which the grains are arranged in eight or more parallel rows."

Collins (1919) is one of the first to have investigated the morphology of the ear in some detail. He brought in a new kind of evidence for this study by working with *Zea-Euchlaena* hybrids. He considered the primary morphological unit of the ear, as well as of the tassel, to be the organs borne in a single metamer of the rachis. In the pistillate inflorescence the members of this morphological unit occupy a single alveolus but since in the tassel the depression is too shallow to be termed an alveolus he proposed the word "alicole" to "designate the spikelet or spikelets, whether staminate or pistillate, that are borne in a single alveolus or at a single point on the rachis, considered as the axil or point of attachment of a reduced branch." According to Collins, there is evidence that the association of alicoles into pairs, "yoked alicoles," is more fundamental than their linear arrangement. In discussing dropping out of rows on the ear, Collins concluded that the dropped rows are on the opposite side of the ear and that this could occur if the two pediceled spikelets were dropped simultaneously from a pair of yoked alicoles. Weatherwax (1935) has shown that the rows of grains on the cob are paired because the spikelets are paired and has shown that the dropping of rows in the ear is due to one or more rows of paired spikelets having been discontinued and not to the dropping of one row from each of two or more rows of paired spikelets as Collins assumed.

Each of the paired spikelets consists of two florets, the lower floret usually aborting. However, in certain corns such as the sweet variety, Country Gentleman, both florets are often fertile, and Weatherwax (1935) showed that the crowding thus brought about by the extra grains breaks up the linear arrangement of rows and produces ears without distinct rowing.

Certain abnormalities of the ear have been described as, for instance, reversed kernels where the germ faces in a different direction from the normal. This condition was noted by Kellerman in 1891.

Studies of the early morphological development of the ear have been made by Fujita (1939) and Bonnett (1940). Fujita showed that in ears having odd number of pairs of rows (10, 14, 18, etc.) the rows tend to be twisted but that with even pairs of rows (8, 12, 16, 20) they tend to be straight. He is also the first to publish illustrations of thin cross-sections of the young developing ear. Bonnett (1940), by dissecting out young inflorescences in various stages, has presented a clear picture of the development of the superficial features of the ear. He has shown that the spikelet-forming branch initials divide into two unequal parts to form spikelet initials which then divide into two unequal parts to form the flower initials. In the ear the flower developing from the larger (upper) flower initial becomes fertile and the smaller (lower) one aborts in those corns in which there is a single fertile flower per spikelet. Subtending each spikelet-forming branch is a ridge which increases in size and forms the cupule in which the spikelets are borne.

Cutler (1946), one of the most recent authors who has studied the maize ear, stresses the point that the general opinion still persists that the origin of the ear must have been something unique and nearly miraculous. He discusses a number of grasses which do not ordinarily bear ear-like structures but on which they are found occasionally. These he shows are the result of fasciation. He does not imply, however, that these grasses are directly concerned in the evolution of maize but merely uses them as examples to show that the development of the ear and tassel may not be as unique a phenomenon as it is usually thought to be. He also describes an interesting arrangement of spikelets and alveoli found in a South American corn in which the alveoli, instead of having the linear arrangement as in other corns, are arranged like bricks in a wall.

Cutler also stresses the need for a careful comparative study of the ear. If a number of ear characters can be found which could be used in the classification of corns, he points out, it would be possible to include in the studies of the origin and distribution of the various races of maize the vast number of prehistoric ears which the archaeologists have collected.

METHODS

Any one who has handled mature corn cobs is aware that they may be very hard and tough and that some are almost impossible to break with the bare hand. Because of this excessive hardness it is necessary to devise a method whereby serial series of sections could be obtained thin enough for microscopic study. A modified celloidin method was developed which worked well with all materials used including prehistoric cobs from archaeological sites.

Ears of the desired varieties were shelled and the cob boiled for several hours in water to which had been added a few cc. of an aerosol solution. The solution is very effective in small quantities and was prepared by dissolving a small amount of American Cyanamid & Chemical Corporation "Aerosol OT," 100 per cent, in methyl alcohol and then adding an equal amount of water. The only precaution to be taken in its preparation is that the solid aerosol be dissolved in the alcohol before the water is added. The addition of a few cc. of this stock solution has the effect of lowering the surface tension of the water sufficiently so that dry cobs would wet immediately and sink, consequently reducing the time required for boiling. This thorough wetting of the cob made it possible to remove certain gummy substances which were not removed when they were boiled in water without the aerosol. After boiling, the cobs were washed in running tap water for several minutes and then cut into sections small enough to clamp into the microtome. Even after boiling it was often necessary to use a hammer and a heavy scalpel to cut the cob into sections. Small cobs were cut crosswise into sections approximately one inch long. Larger cobs were cut longitudinally into quarters or halves depending upon their size.

The material was dehydrated by running it through an alcohol series using 30, 70, 95 and 100 per cent strengths. Material was left in each of the various grades of alcohol 24 hours.

Two celloidin methods were tried, the regular one as outlined by Chamberlain (1932) and the Rapid Embedding Low Viscosity Nitrocellulose Method outlined by Koneff and Lyons (1937). Results obtained by either method were satisfactory, but since the latter is more simple and more rapid it was the one used in this investigation.

After dehydration the material was placed in a solution of equal parts of absolute alcohol and ethyl ether, where it was allowed to remain for one hour. It was then placed in small wide-mouthed bottles and a 10 per cent nitrocellulose solution added, after which the corks were securely wired in place and the bottles placed in a paraffin oven for 24 hours. The pressure built up in the bottles facilitates the infiltration of the nitrocellulose solution into the plant material. After removal from the oven the bottles were allowed to cool before opening. The 10 per cent nitrocellulose solution was then poured off and a 25 per cent solution added, after which the corks were secured and the bottles again placed in the oven. The following day a 50 per cent solution was added and the bottles placed in the paraffin oven as before. Upon cooling they were opened, and the material picked up by means of forceps and quickly plunged into chloroform where it was allowed to remain for 24 hours in order to harden the nitrocellulose. The chloroform was changed once during the 24 hours. Later the hardened blocks containing the embedded material were placed in 80 per cent alcohol where they were allowed to remain until sectioned.

All sectioning was done with a Bausch & Lomb sliding microtome. Because of the differences in the density of the tissues of the cob, microtome blades must be exceptionally sharp. All the blades used in this investigation were either sent to the factory or to a professional instrument grinder for sharpening. The number of sections obtained before resharpening of the blade is necessary varies with the hardness of the cob but usually from three to five cobs may be cut before the blade needs to be resharpened.

The nitrocellulose blocks were removed from the alcohol and excess embedding material was removed after which the blocks were clamped directly into the microtome. During the cutting the knife and block containing the embedded cob were kept flooded with 80 per cent alcohol, this being accomplished by "painting" them with a small camel's-hair brush dipped into the alcohol. Sections were prevented from curling by holding the brush on the surface of the block as they were cut. The individual sections were removed with the same brush and placed in the alcohol.

All staining was done with safranin and light green. Before staining, the nitrocellulose was removed from the plant material by placing the sections in equal parts of ether and absolute alcohol in small culture dishes for approximately 10 minutes. They were then washed in 95 per cent alcohol and placed in a dish containing water to which was added a few drops of a standard safranin solution (1. g. safranin, 100 cc. 50 per cent alcohol). Sufficient safranin was added to give the water a light pink color. The material was left in this stain over night

and the following day the sections taken out and the excess stain removed by placing them in 95 per cent alcohol to which had been added two drops of concentrated HCl per 100 cc. alcohol. The sections were destained until only a slight pink color remained in the parenchyma cells after which they were washed in 95 per cent alcohol and counterstained in light green dissolved in clove oil. Enough stain from the stock solution (1 g. light green, 100 cc. clove oil) was added to pure clove oil so that the sections would be sufficiently stained in one minute. They were then washed quickly in absolute alcohol, cleared in xylol, and mounted in Canada balsam.

Cobs from archaeological sites were handled in the same way except that after being boiled they were placed in hydrofluoric acid for a few days to dissolve any sand that might be present. The hydrofluoric acid was diluted to 50 per cent with water and placed in paraffin containers. The cobs were then placed in the acid and the containers placed under a hood. On removal from the acid the cobs were thoroughly washed in tap water, dehydrated, and handled like the other material.

TOPOGRAPHY OF THE MAIZE COB

It is difficult to interpret the morphology of an ordinary corn cob because its main features are obscured by the papery edges of the floral parts. Even under a dissecting microscope the cob (pl. 37, fig. 1) appears to be a mass of crowded wrinkled chaff of no apparent significance and with the mature cob it is difficult to remove enough of this tissue paper veil without at the same time destroying the underlying structures. Weatherwax (1935) prepared cobs for study by turning them in a lathe and removing all parts down to the hard rachis. Reeves (1946) successfully prepared cobs for study by treating them with sulphuric acid for twelve hours and then washing them in water.

One of the best places to study the surface of the cob is in the corn field. In young growing ears which have been fertilized but are not yet fully mature it is possible to snap off the spikelets with the fingers, leaving the rachis free from the parts that make the mature cob so difficult to study. A morning spent in examining young ears in a large collection will disclose the great variation to be found in the surface features of the cob. Corns possessing the gene (Vg) for vestigal glumes produce ears in which the glumes are so reduced that it is possible to study (pl. 37, fig. 2) the surface features of the rachis without any preparation. The outer glume, while present, is greatly reduced and the lemmas and paleae are almost completely suppressed, thus producing a cob with none of the chaff that makes ordinary cobs so difficult to study.

A typical ear of *Zea Mays* may be said to consist of a more or less elongated cylinder of hardened tissue (the cob) to which are attached pairs of fertile spikelets, usually borne in longitudinal or somewhat spiral rows. If the grains are removed, as well as the chaff and the glumes, to the point where the spikelets are attached to the rachis, it will be seen that the pairs of florets are attached near the lower outer edge of a depression or alveolus that extends into the thickened rachis.

Sturtevant (1899) called this depression a "cupule." Harshberger (1893) wrote, "spikelets . . . placed in a cucullate depression on a fleshy cob." Collins (1919) proposed the word "alicole" to designate "the spikelets, whether staminate or pistillate, that are borne in a single alveolus or at a single point on the rachis, considered as the axil or point of attachment of a reduced branch." Cutler (1946) recently has used alicole in a slightly different sense, thus: "each pair of grains arises from a pair of spikelets and comprises with the related parts of the cob the alicole." For brevity and clarity it is desirable to have a single word for the structure which has been called the "cucullate depression," "corneous cupule" or "alicole" by the different authors. Since alicole has been used in different ways it seems best to follow Sturtevant and call the structure a cupule. Throughout this discussion the word "cupule" will be used to designate the depression or alveolus on the cob near the base of which the paired spikelets are attached.

Weatherwax (1935) has shown that the pairs of spikelets on the ear not only maintain a linear relationship but also a lateral one, and he showed that the spikelets of one row were not opposite those of the adjacent row but alternate with them. He also showed that the dropping of rows in the ear is due to one or more rows of paired spikelets having been discontinued and not to the dropping of one row from each of two or more rows of spikelets as Collins (1919) had assumed. Cutler (1946) has described a race of maize from South America in which the cupules are arranged like bricks, each being covered with half a cupule from the right and half a cupule from the left, thus forming an ear with cross-spiralling of the rows. In other words, rows can be traced in a spiral around the ear in two directions. Thus a single grain will be part of a row that spirals to the left and also part of a row that spirals to the right.

Cupules are not unknown in other grasses. They are conspicuous in such genera as *Manisuris*, *Hackelochloa*, and *Tripsacum*. St. Augustine grass (*Stenotaphrum secundatum* (Walt.) O. Kuntze) bears rows of solitary fertile spikelets in cupules on a corky flattened rachis (Cutler, 1946). On close examination it will be seen that the cupules of different varieties of maize vary greatly in shape, in the depth to which they penetrate into the cob and in the development of tissue on the sides above the attachment of the spikelet pairs. In some varieties the cupule is shallow and almost saucer-shaped while in others it is much wider than it is high and penetrates deeply into the rachis. In many of the corn-belt varieties the cupule not only penetrates deeply into the rachis but tends to turn up at an angle. According to Bonnett (1940) the cupule develops from a ridge subtending the spikelet initials and is similar to the subtending leaf initials that appear in the differentiation of the inflorescence of barley, wheat, and oats. The development of the outer edge of the cupule was mentioned by Harshberger (1893) in describing *Zea Mays:* "spikelets paired in alveoli, strongly marginal and cupulate, the margins becoming hard and corneous." Arber (1934) has used the term "rachilla-flaps" for the non-vascularized outgrowths of the reproductive axis of certain grasses and has given as an example the outgrowths of the lip of an oblique cupule in

Cephalostachyum virgatum Kurz., an east Indian bamboo. Cutler (1948) has called the outgrowths of the margin of the cupule in maize, "rachis-flaps," and that term will be used in the following discussion. In certain races of maize the rachis-flaps are little developed and form only a slight ridge separating the cupules from the adjacent parts of the cob. In other races the rachis-flaps form very conspicuous outgrowths at the side of the cupule which may be several mm. in length, as, for example, the Mexican variety Cacahuazintle, which has rachis-flaps as much as 5 mm. in length and is flexible due to the presence of only a small amount of sclerenchyma. In varieties with highly sclerenchymatized cobs the rachis-flaps are usually hard and corneous.

Another variation apparent in cross-sections of the cob is the manner of insertion of the spikelet pairs on the cob axis. This is affected to a certain extent by the development of the rachis-flaps as well as by the depth of the cupule. Cross-sections of certain varieties show the spikelets attached directly to a more or less cylindrical rachis, while other corns, especially United States corn-belt varieties, have the spikelets attached at the bottom of a cup-like depression. A closer inspection will disclose that this difference is due to the fact that in the first case the cupule is very shallow and the rachis-flaps only slightly developed while in most corn-belt varieties the cupule is well developed and extends a considerable distance into the rachis and the rachis-flaps tend to be well developed.

The length of the pedicels of the spikelets varies in different races of maize and has been mentioned by various investigators (Mangelsdorf & Cameron, 1942; Cutler, 1946). In some races of corn such as the northern flints as defined by Brown and Anderson (1947) the spikelets are attached by a broad base to the lower margin of the cupule so that there is no definite line of separation between the glumes and the cob. In certain varieties from South America and from Asia the spikelets are distinctly pedicellate, and the pedicels may be up to 2 mm. in length.

INTERNAL ANATOMY

Just as the cob varies in its surface features, so it also varies in its internal features. Cross-sections show great variation in the proportion of sclerenchyma and pith. Four distinct zones may be differentiated in the cross-section of an average corn-belt cob as follows: (1) Immediately inside of the epidermis there is a more or less solid ring of thick-walled lignified cells inside of which there is, (2) a cylinder of pith composed of large thin-walled parenchyma cells. Lying embedded in these two zones is (3) the vascular network which, at least in certain races of maize, consists of two rather distinct tubes of vascular bundles, one inside of the other (Reeves, 1946; Laubengayer, 1946). Their location relative to the other zones will be discussed more fully later. (4) The fourth zone consists of branched parenchyma cells which surround the vascular bundles as they leave the inner vascular tube and extend out into the spikelets.

Sclerenchyma.—

The texture of the cob, whether fibrous and flexible or lignified, hard and stiff, depends to a large extent upon the relative amount of sclerenchyma contained. Most North American corn-belt varieties have a hard tough cob. The cross-sections of such types show a well-defined sclerenchyma zone forming a nearly solid tube between the epidermis and the pith. It is within this mass of thick-walled cells that the cupules are located and in such varieties the rachis-flaps, as well as the outer glumes of the spikelets, tend to be heavily sclerenchymatized. There are other races of maize which tend to have rather soft cobs, as, for example,

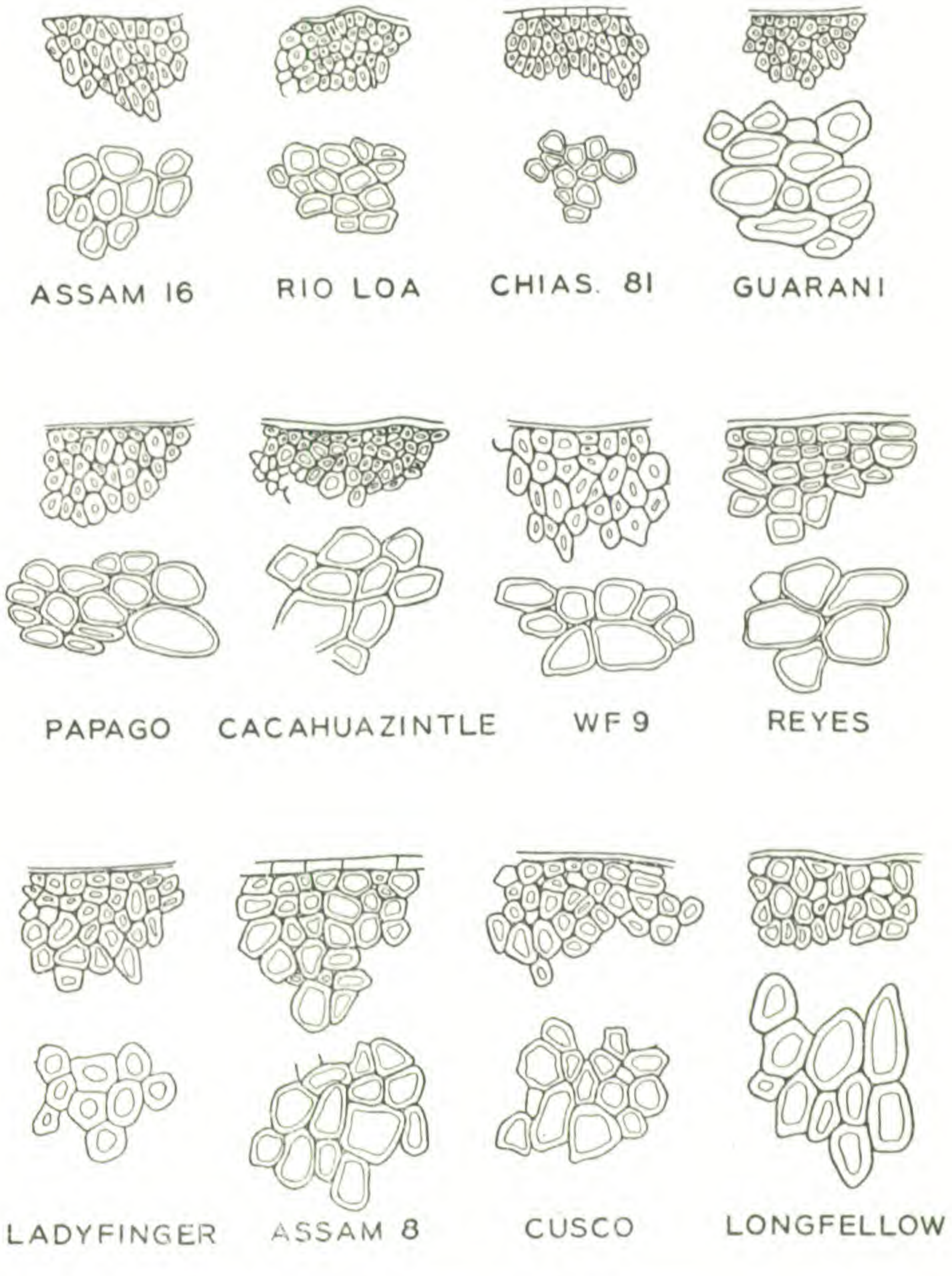

Fig. 1. Camera-lucida drawing of sclerenchyma. In each case upper drawing shows cells from immediately under the epidermis, lower drawing shows them half way between the epidermis and the pith.

certain South American varieties which are so delicately constructed that one can push the grains into the cob with the finger (Mangelsdorf & Cameron, 1942). In such cobs the sclerenchyma is present only as a relatively thin layer surrounding the cupules, and the rachis-flaps tend to be sclerenchymatized only on their inner face, while the glumes (Cutler, 1946) may even be delicate membranes.

The sclerenchyma tissue itself varies considerably in different corns. The cells may be relatively small and densely packed or larger and rather loosely packed. The distinction between sclerenchyma cells and pith cells, while abrupt and distinct in most corns, may show a rather wide area of transitional tissue where the cells become progressively larger and less thick-walled as they approach the central pith area.

Within any one cob the shape of the sclerenchyma cells varies greatly depending on their location. Both sclereids and fibers are found. According to Eames and MacDaniels (1947), the classification of sclerenchyma into sclereids and fibers has no morphological significance and is only used for convenience in description. In the sclerenchyma of the cob there is every gradation from typical fiber cells many times as long as wide to isodiametric sclereids. They may be smooth in outline or variously lobed. One unusual type of cell present in the cob is the branched parenchyma cell discussed in detail below. In some areas these cells become thick-walled and lignified and can thus be termed "astrosclereids." The size of the sclerenchyma cells and the amount of thickening of the cell wall vary in different races of corn as shown in fig. 1. The pits are small and the pit canals are usually unbranched. This character, as shown by Eames and MacDaniels (1947), is of little value in classification, being dependent to a large extent upon the thickness of the cell wall.

Pith.—

Nearly all corn cobs possess a central cylinder of pith. Prehistoric cobs often appear to be hollow, due to the decomposition of the soft parenchymatous tissue that originally filled the center of the cob. In general, the pith is rather uniform in the different races of maize, the cells being nearly isodiametric and thin-walled. However, the cell size varies in different corns, some varieties having more and larger intercellular spaces than others. As has already been mentioned, there is sometimes a rather wide area of transitional cells between the thick-walled sclerenchyma and the thin-walled parenchyma. There is also an area of transitional cells between the regular parenchyma pith cells and the highly branched parenchyma cells which form the sheath around the vascular bundles as they enter the spikelets. In the cobs of certain corns there may be a ring of cells in the pith which are colored and slightly thicker-walled than the surrounding pith cells. These are the so-called "pith-rings" of the corn-breeders. Pith-rings are commonly found in North American corns and have also been found in early prehistoric corn from Arica, Chile.

Vascular System.—

It has been difficult to obtain a complete understanding of the vascular system of the corn plant because of the difficulty in making preparations of certain portions, especially of the node and ear. Evans (1928), in discussing the vascularization of the node of *Zea Mays,* wrote:

> "Imbedding of tissue from the node and then sectioning has been found inadequate in the study of the node, since the branching of the vascular bundle is so intricate and the branches so tortuous as to defy solution even in the best prepared serial sections."

He developed a method of staining the vascular bundles in the stalk and then subjecting the sections to retting action by bacteria. After removal of the decomposed parenchymatous cells he was able to study the vascular network of the node of the corn stalk. He concluded that single vascular bundles seldom pass through more than two or three nodes without branching and further that "so complicated does this branching become that it is impossible of tracing even when no other tissues are present to complicate the situation."

Reeves (1946), in studying the vascular system of the mature ear, also used a retting process involving cellulose-digesting microorganisms. He was able to separate the vascular system from the other parts of the cob. Laubengayer (1946), using much the same technique, studied the vascularization of the cob of a northern flint. He showed that the vascular arrangement of the shank was essentially that of the main stem. However, in the transitional region from shank to ear the bundle system reorganized itself into two distinct systems, one inside of the other. The inner vascular system, with its larger bundles, supplies the spikelets, while the outer tube of smaller and more-branched bundles supplies the other parts of the cob. This arrangement of the bundles as shown by Laubengayer differs from that described by Weatherwax (1935), who says that the vascular bundles of the cob are distributed in approximately the same manner as those of the stem except for a tendency toward peripheral arrangement. Laubengayer's interpretation would seem to hold true for the majority of the cobs examined in this investigation. There are, however, varieties in which the vascular bundles are more or less evenly distributed throughout the pith of the cob, as, for example, in the inbred line Illinois R4, and in such cases it would appear that the inner vascular system would then form more of a cylinder of vascular bundles rather than the hollow tube of bundles as demonstrated by Laubengayer for the northern flints. That these two vascular systems are not entirely free from one another has been shown by Cutler (verbal communication). He was able to find small branches which connect the two systems at the nodes and he also found that a bundle that is originally a member of the inner system may later become a member of the outer system.

The location of the two fibrovascular systems relative to that of the sclerenchyma tissue varies greatly. In general, in cobs with large amounts of sclerenchyma, as, for example, those of the North American corn-belt varieties, the outer vascular system lies embedded within the sclerotic tissue. The inner cylinder, the

one supplying the spikelets, tends to lie along the line separating the sclerenchyma from the pith. Some bundles, however, may be located in the pith a slight distance from the sclerenchyma layer, in which case there may be a lobe of sclerenchyma tissue extending into the pith and surrounding the bundles with a sheath of sclerenchyma tissue a few cells thick. Since all the bundles are surrounded by a sclerenchymatous bundle-sheath it would appear in some cases that this lobe of sclerenchyma tissue does not actually surround the bundle itself because the layer of sclerenchyma cells around the bundle is no thicker than that found in the regular bundle-sheath. In some varieties such as inbred line Illinois R4, a considerable number of vascular bundles will be found distributed throughout the pith zone. In most corns some vascular bundles of the inner system will be found embedded within the sclerenchyma.

In races of corn which have cobs less sclerenchymatized than the rather extreme corn-belt varieties, the outer vascular tube tends to occupy the parenchymatous areas lying between the masses of sclerotic cells.

The vascular bundle of the corn plant has long been used in elementary classes as a typical example of a vascular strand, and since so many writers (Hayward, 1939, Holman & Robbins, 1939) have described the cells of which it is composed it need not be discussed here. No essential difference is found in the structure of the bundles of the two systems except that of size.

Branched Parenchyma.—

One of the most unusual types of tissue found in the maize cob is the branched parenchyma cells which are located between the sclerotic tissue and the vascular strands near the base of the spikelet and extending some distance into it. According to Eames (personal communication) the presence of these cells in corn is surprising, as is also their location. The inner edge of this zone lies near the inner vascular system, and cells transitional between pith parenchyma and the branched parenchyma may be found. The branched parenchyma cells tend to be considerably smaller than the pith parenchyma cells and are usually somewhat elongate with numerous branches, although they may be almost stellate in shape. The tips of the branches often are enlarged and may be nearly twice the diameter of the rest of the branch. The cell walls of these cells are usually thin but near the sclerotic zone some of the cells may be lignified, and in such cases they could be classified as "astrosclereids."

DISCUSSION

Of the anatomical and histological characters of the cob which are capable of exact measurement three characters vary greatly between the different varieties, namely, (1) The rachis-flaps, (2) the length and shape of the pedicels, and (3) the amount and distribution of the sclerenchyma.

(1) *Rachis-flaps.*—One of the most conspicuous differences in the cross-sections of the various varieties of maize is found in the rachis-flaps which vary in

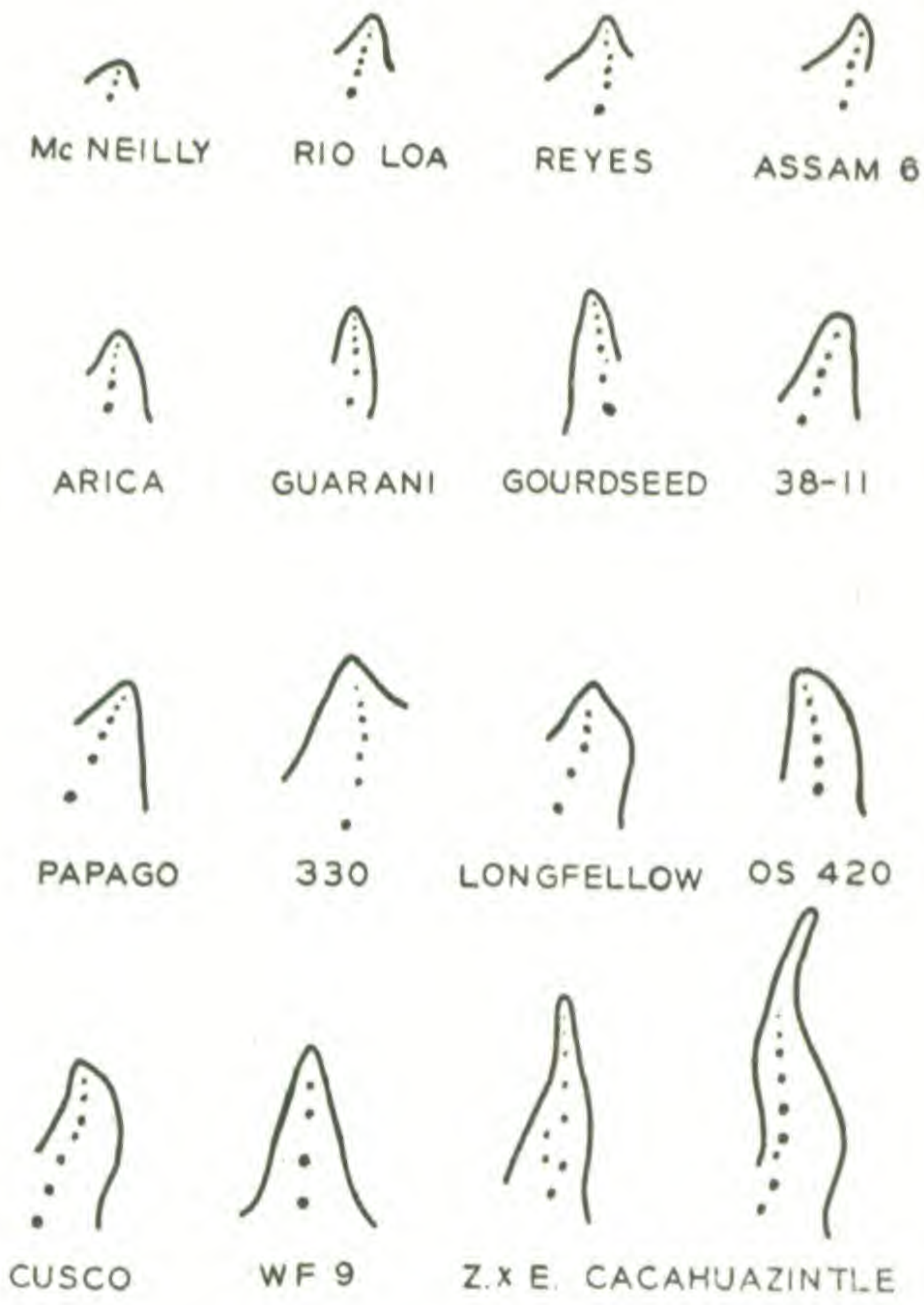

Fig. 2. Outline drawings of cross-sections of rachis-flaps made at the point of greatest development. Black dots are vascular bundles.

both size and shape. As defined in this paper, rachis-flaps are the outgrowths from the side of the cupule. They vary from a slight ridge separating the cupule from the adjacent parts of the cob (as, for example, in Ladyfinger popcorn) to the extremely long flexible appendages found in the Mexican variety, Cacahuazintle. To obtain an exact measure of the rachis-flaps, their outline was traced on paper from prepared cross-sections by means of a Bausch & Lomb microslide projector. The extent of variation of this character is shown in fig. 2. It is evident that Ladyfinger, Rio Loa, Reyes, Bolivia and Assam #6 and the prehistoric Arica varieties have the least developed rachis-flaps and that the most strongly developed ones are found in North American and Mexican varieties—inbred line WF 9, *Zea-Euchlaena* back-crossed to *Zea,* and Cacahuazintle.

From the varieties so far studied it would appear that the presence of well-developed rachis-flaps is due to *Tripsacum* contamination. The evidence for this, while not conclusive, is suggestive. Except for Cacahuazintle, the greatest development of rachis-flaps is found in the *Zea-Euchlaena* cross and all other varieties possessing well-developed rachis-flaps also show other tripsacoid characters. Cacahuazintle is a high-altitude Mexican variety. From the criteria advanced by Mangelsdorf and Reeves (1939) Cacahuazintle would in general be non-tripsacoid.

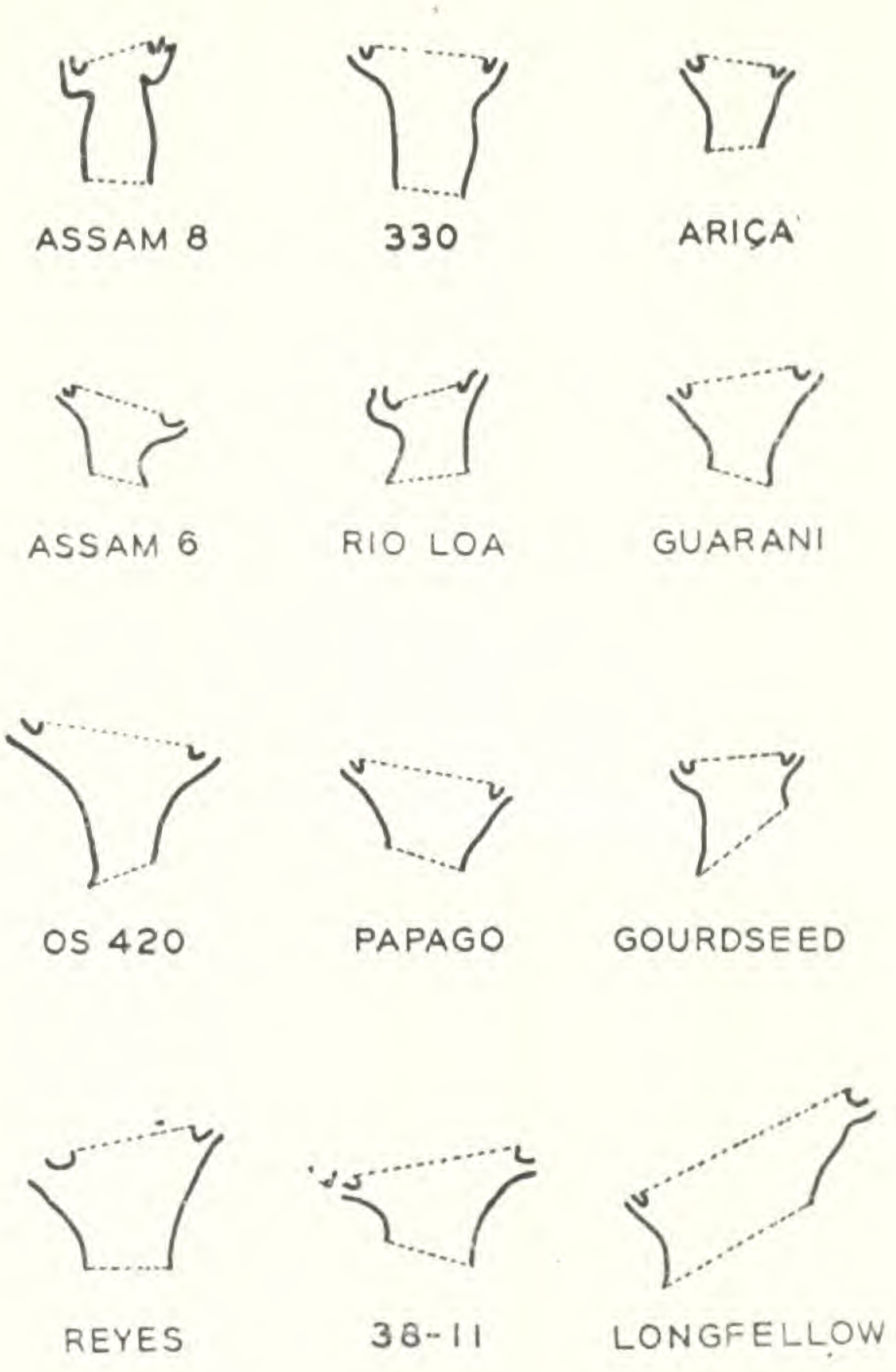

Fig. 3. Camera-lucida drawings of longitudinal sections of pedicels and glume bases.

The development of the excessively long rachis-flaps might be explained as due to an extreme recombination of characters derived from *Zea* and from *Tripsacum*.

(2) *Pedicel Length*.—As has already been mentioned by several authors (Mangelsdorf, 1945; Cutler, 1946) the length of the pedicel varies in different varieties of maize. They have described the long pedicels found in certain South American varieties. The pedicel not only varies in length but also in width and in shape; some of the South American and Oriental varieties have long and thin pedicels while other varieties may have equally long but relatively much thicker ones. In order to obtain a measure of this character slides were projected as before and the outline of the pedicel traced on paper. Since length and thickness are both important, the length of the pedicel was divided by the width in order to arrive at a significant measure of the relative length and thickness of the structure. Results are shown in fig. 3. The longest pedicel found in any variety studied was in Assam #8 (see pl. 38, fig. 6). In this variety the pedicels are rather thin and may be as much as 2 mm. in length, equal to any reported by Cutler for Andean corn. The fact that the pedicels are borne in a shallow cupule makes their length more noticeable than if the cupule were deep. In the commercial four-way hybrid, Pioneer 330, which has rather extremely long pedicels for North American corn,

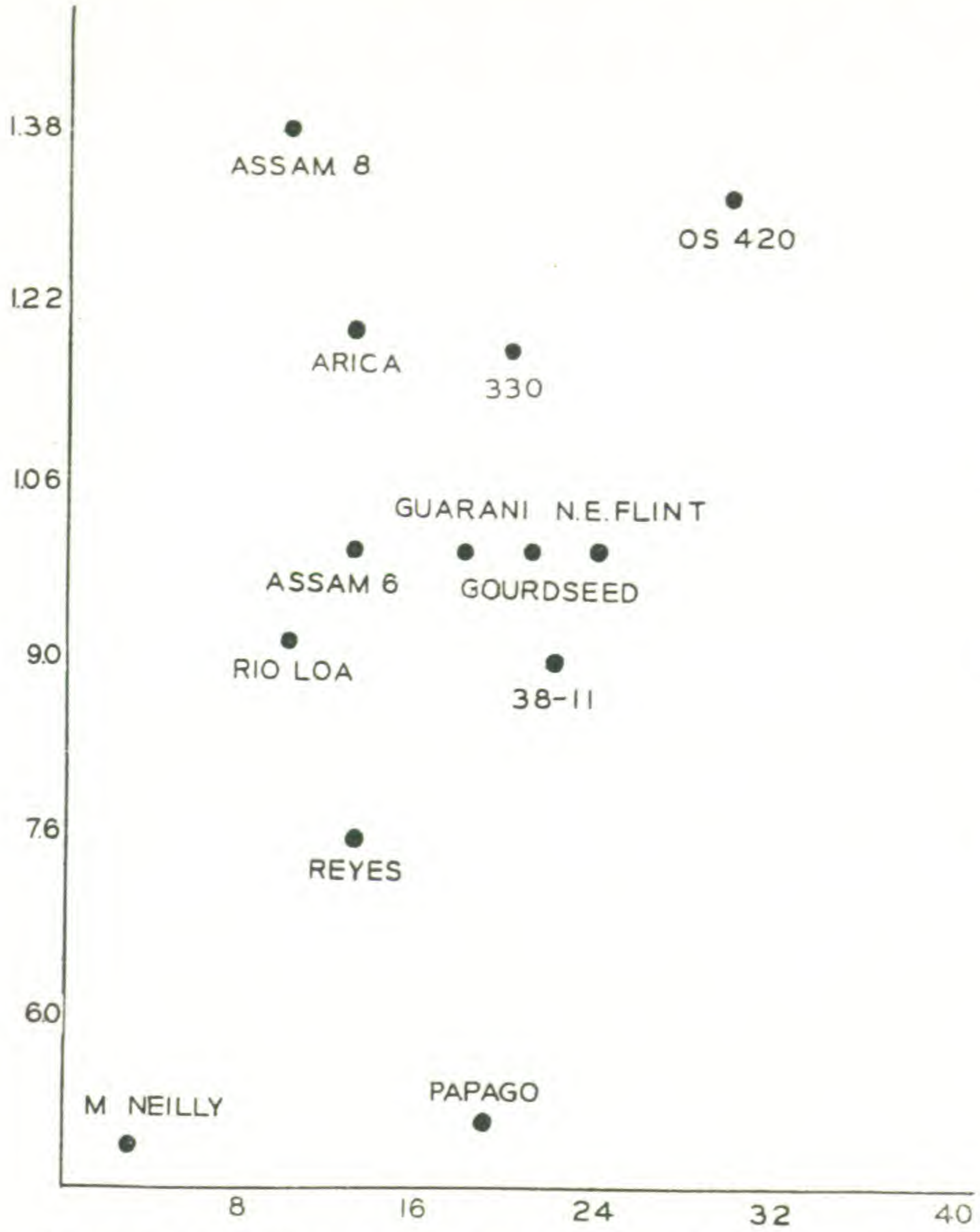

Diagram I. Scatter diagram showing relationship between pedicel length and length of rachis-flaps: horizontal axis, length of rachis-flap in mm.; vertical axis, pedicel length in per cent of pedicel width. Note that "McNeilly" in diagram is referred to as "Ladyfinger" in the text.

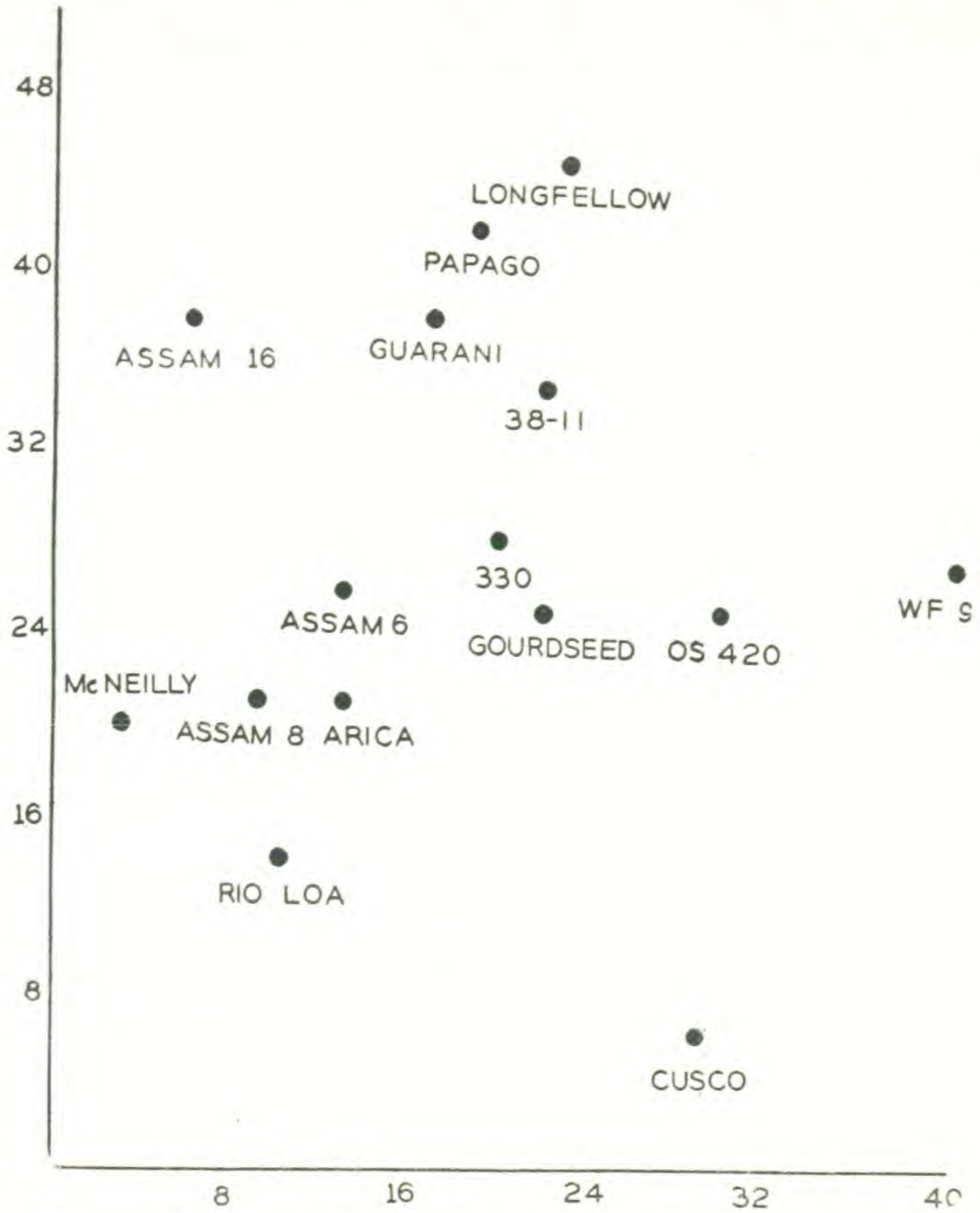

Diagram II. Scatter diagram showing relationship between rachis-flap length and per cent of sclerenchymatization of the cob: horizontal axis, rachis-flap length in mm.; vertical axis, per cent of sclerenchymatization of cob.

they are less conspicuous than in the South American and Oriental varieties since they are set in a deep cupule. The pedicels in Pioneer 330 are also broader in relation to their length than those in Assam #8. Among those varieties having short and thick pedicels are Gourdseed, Longfellow and New England Flint. According to Cutler (1946) one of the most obvious effects of tripsacoid influence is the shortening of the pedicels and the sinking of the whole spikelet into the cupules.

(3) *Sclerenchyma.*—Stained sections show great intervarietal differences in the amount of sclerenchyma. This is noticeable from stained slides even without the use of a microscope. Since the distribution of the sclerenchyma, as well as the amount, varies from variety to variety, it was necessary to measure the differences in the same relative place on all the cobs. After some preliminary trials it was decided to measure the thickness of the sclerenchyma at the point where the cupule extended the greatest distance into the cob. Slides of cross-sections were projected and the outline of the cupule traced showing the extent of the sclerenchyma. This was then divided by the radius of the cob at that point. This was called the degree of sclerenchymatization of the cob. It varies in the different varieties from 5 to nearly 50 per cent of the cob at the point measured. Since this character varies considerably within a single cob all sections used for comparative study were from near the center of the cob.

The least sclerenchymatized variety studied is Chiapas #81 (Rockefeller Foundation collection number), a flexible-cobbed variety. Here the sclerenchyma forms only a thin layer surrounding the cupule. Other varieties possessing small amounts of sclerenchyma are Rio Loa, Cusco, Assam #8, Arica and Ladyfinger popcorn. Among the most highly sclerenchymatized varieties are Longfellow, Papago, Guarani and inbred line 38-11. According to Mangelsdorf and Cameron (1942) *Tripsacum* contamination tends to impart a coriaceous quality to all parts of the cob. Of the highly sclerenchymatized varieties studied all possess other characters which would indicate that the variety is highly tripsacoid.

SUMMARY

1. The anatomy of the female inflorescence of *Zea Mays* (the corn cob) is of importance in corn-breeding, in studies of archaeological maize, and in considering the phylogeny of maize and its relatives.

2. Thin sections of mature corn cobs, both of recent and archaeological material, were prepared by a modified celloidin technique which is described in detail.

3. The topography of the mature cob is described. The main features of the cob surface are: The paired spikelets, (b) the associated cupule (or alveolus) and (c) the outgrowths from the side of the cupule, the rachis-flaps. The pedicels of the spikelets vary greatly in different varieties of maize, both in length and in shape. Certain varieties have pedicels as much as 2 mm. in length. Cupules vary from shallow depressions on the rachis, to deep cavities

penetrating a considerable distance into the cob. The rachis-flaps vary from slight ridges separating the cupule from the adjacent parts of the cob to long flexible appendages as much as 5 mm. long.

4. In cross-sections of mature cobs four distinct types of tissue are found, exclusive of the epidermis. They are: (a) A sclerenchyma zone, (b) a cylinder of pith, (c) the highly branched vascular system which consists (at least in certain varieties) of two rather distinct cylinders of vascular elements one inside of the other. The inner system supplies the spikelets and the outer system supplies the other parts of the cob, and (d) branched parenchyma cells which surround the vascular strands as they leave the inner vascular cylinder.

Great variation exists in the amount and location of the sclerenchyma in the cob, and varieties with "soft" cobs are shown to contain smaller amounts of sclerenchyma than "hard" cobs. The location of the inner vascular system varies but tends to occupy the area between the pith and the sclerenchyma. The outer vascular system is embedded within the sclerenchyma in highly sclerenchymatized varieties and the area between the masses of sclerenchyma in varieties which are only slightly sclerenchymatized. Nearly all cobs possess a pith center. The size of the parenchyma cells and the number of intercellular spaces vary in different varieties.

5. Three characters were found in the cob which varied greatly between the different varieties of maize, and methods were devised to measure these differences. *Rachis-flaps:* The least-developed rachis-flaps are found in Ladyfinger popcorn, Rio Loa, Reyes, Assam #6 and the prehistoric Arica, Chile, corn. The greatest development of rachis-flaps are in Mexican and North American varieties, Gourdseed, inbred line 38-11, Papago, Longfellow, OS-420, WF-9 and Cacahuazintle. *Pedicel length:* Pedicels vary from short and thick to long and thin. Assam #8, Pioneer 330, Arica, Assam #6 and Rio Loa have relatively longer and thinner pedicels than the varieties, Longfellow, inbred line 38-11, Reyes, and Gourdseed. *Sclerenchyma:* The amount of sclerenchyma in the different varieties of corn varied from 5 to 46 per cent of the radius of the cob at the point measured. The least sclerenchymatized varieties were Cusco, Rio Loa, Assam #8, Arica and Ladyfinger popcorn. The most highly sclerenchymatized varieties were Longfellow, Papago, Assam #16, Guarani and inbred line 38-11.

SOURCE OF MAIZE VARIETIES STUDIED

Arica—Junius Bird, Am. Mus. of Nat. Hist.—from excavations at Arica, Chile.
Assam #6—Naga Hill Tribes, Assam, India.
Assam #8—Naga Hill Tribes, Assam, India.
Assam #16—Naga Hill Tribes, Assam, India.
Cacahuazintle—Rockefeller Foundation Collection, Mexico, D. F.
Chiapas #81—Rockefeller Foundation Collection, Mexico, D.F.
Cusco—Lehman Collection, Cusco, Peru.
Gourdseed—Grapevine, Texas.
Illinois R4—Pioneer Hi-Bred Corn Co., Johnston, Iowa.

LADYFINGER—McNeilly Seed Co.
MCNEILLY—see LADYFINGER.
PAPAGO—L. W. Lenz, Papago Indian Reservation, Sells, Arizona.
PIONEER 330—Pioneer Hi-Bred Corn Co., Johnston, Iowa.
REYES—H. C. Cutler, Reyes, Bolivia.
RIO LOA—Carl and Jonathan Sauer, Chiu Chiu, Chile.
VESTIGIAL GLUME *(Vg)*—DeKalb Hybrid Seed Corn Co., DeKalb, Ill.

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Explanation of Plate

PLATE 37

Fig. 1. Surface view of an ordinary cob showing remaining parts of spikelets. Scarious edges of floral parts conceal nearly all of the surface detail of the rachis. The white broken ends of the pedicels can be seen in a few places.

Fig. 2. Surface view of a cob from plant homozygous for vestigial glume (Vg). Reduction of glumes and lemmas reveals the following surface details: (a) paired spikelets, (b) rachis-flaps clearly seen at center of photograph, (c) alternate arrangement of pairs of spikelets on adjacent pairs of rows, (d) cupule extending into rachis behind the broken ends of the pedicel.

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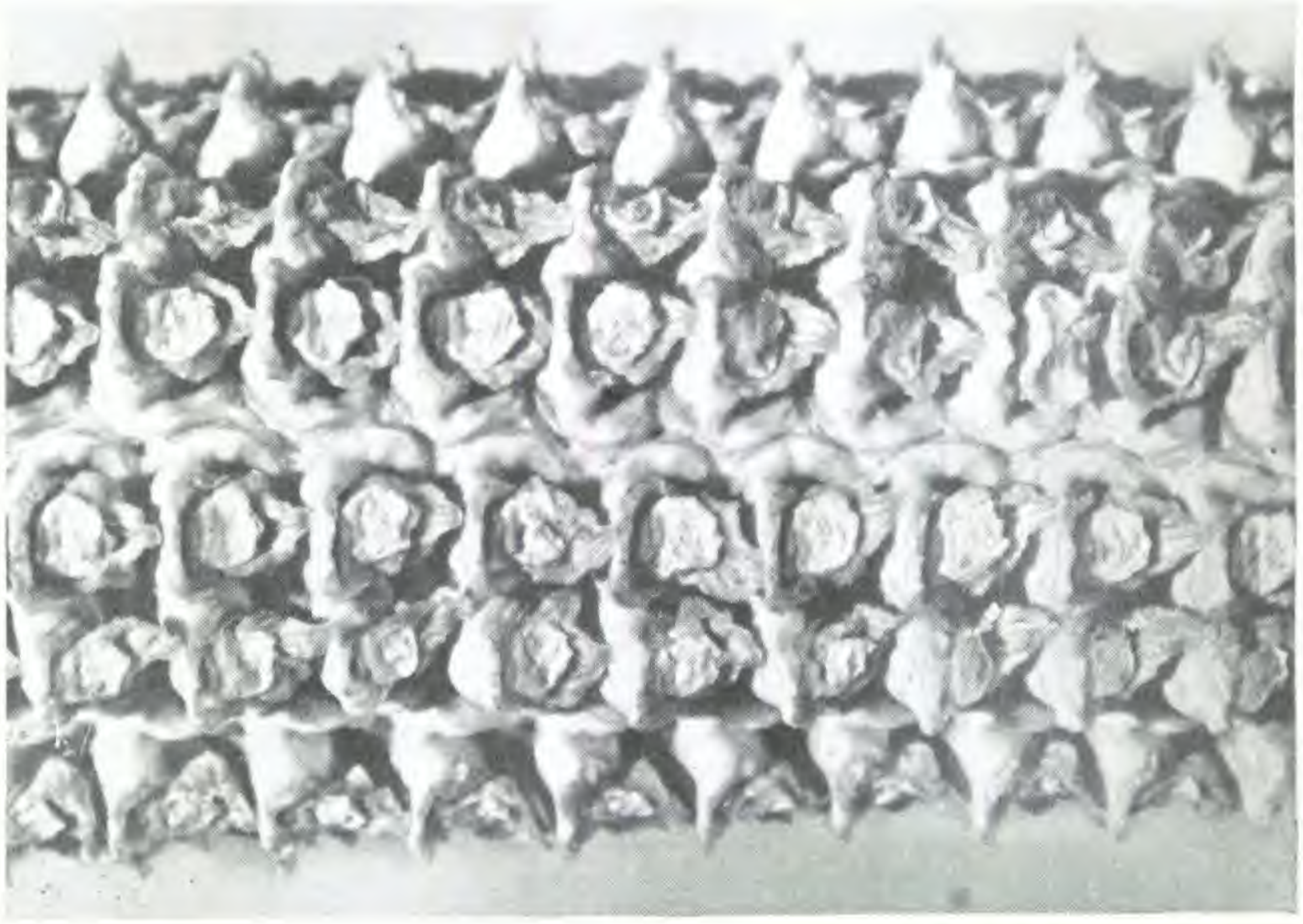

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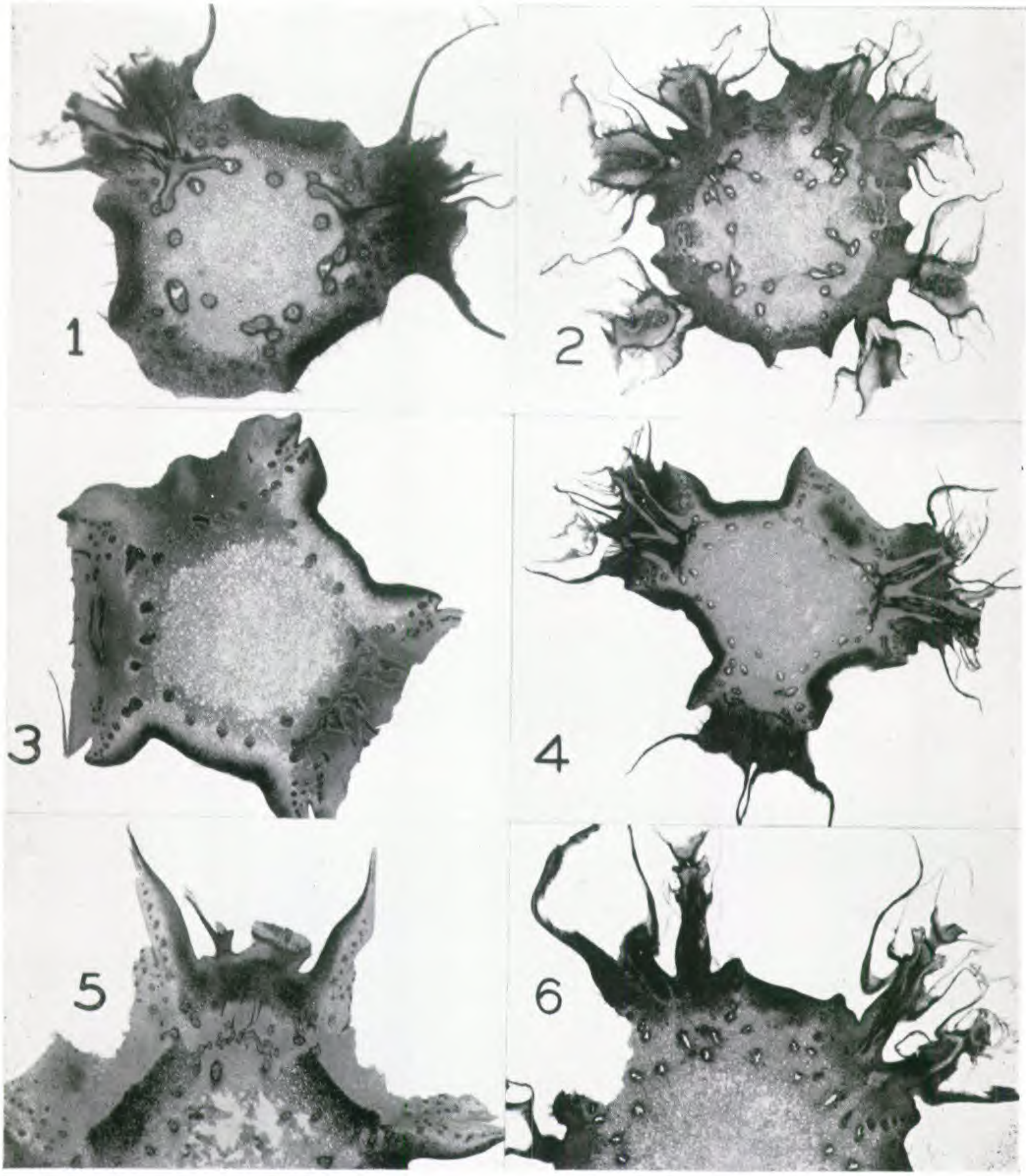
LENZ—HISTOLOGY OF THE CORN COB



LENZ—HISTOLOGY OF THE CORN COB

Explanation of Plate

PLATE 38

Photomicrographs of cross-sections of corn cobs: (1) Ladyfinger, (2) Reyes, (3) Chiapas #81 (flexible cob), (4) Arica, Chile (prehistoric), (5) Cacahuazintle, (6) Assam, India, #8.

EXPLANATION OF PLATE

PLATE 39

Camera-lucida drawings of a serial series of cross-sections of the cob of a United States commercial "hybrid" variety (Pioneer 330). Solid black, dense sclerenchyma; stippled, ordinary sclerenchyma; white, parenchyma.

Fig. 1. Showing pair of spikelets set deep in the rachis.

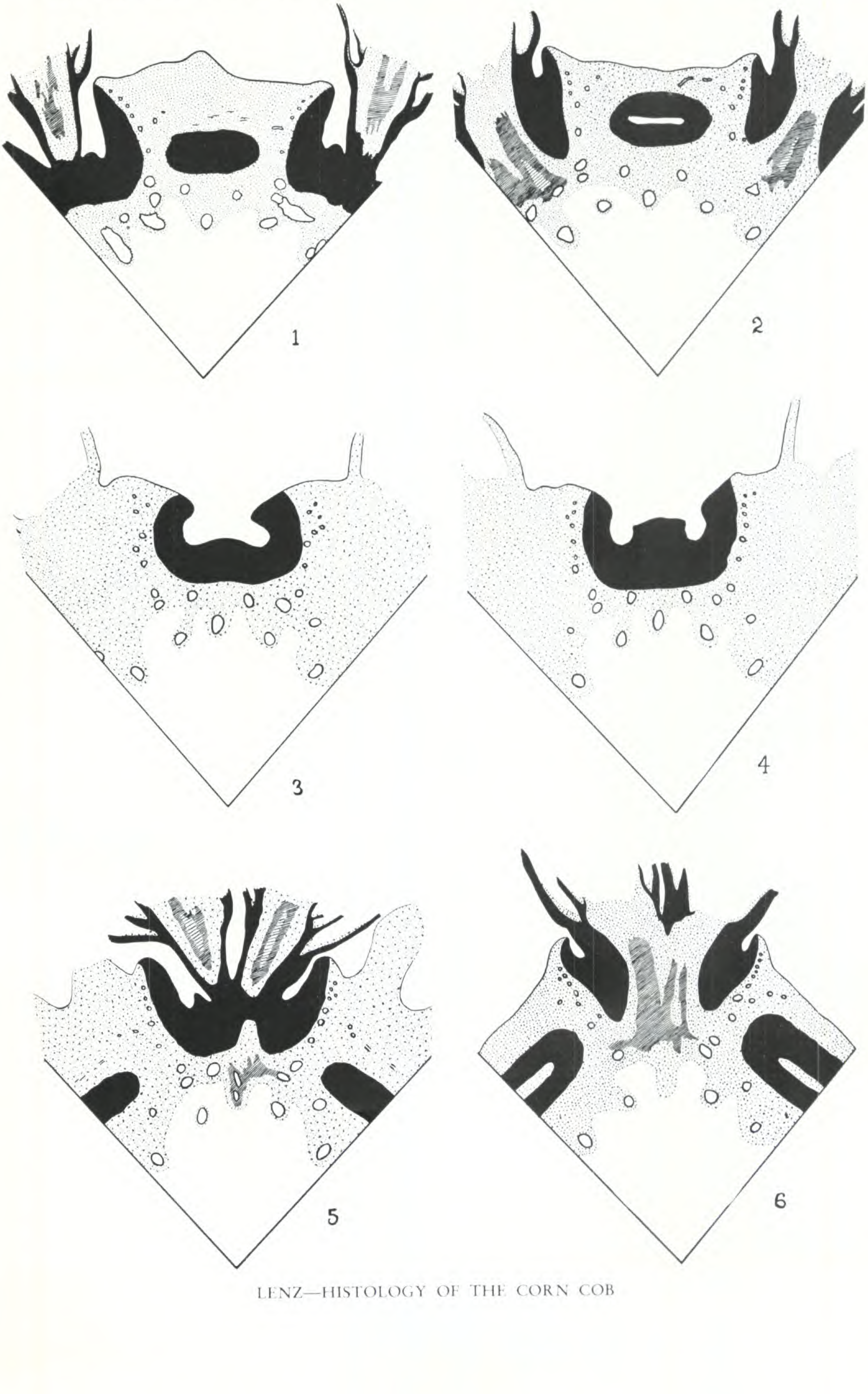
Fig. 2. Beginning of next cupule above and between the spikelets shown in fig. 1; first seen as an area of less dense sclerenchyma inside the center of dense sclerenchyma, later an opening appears in this mass of sclerenchyma.

Fig. 3. Opening which first appears in fig. 2 increases in size outward until it reaches the surface and opens out to form the cupule.

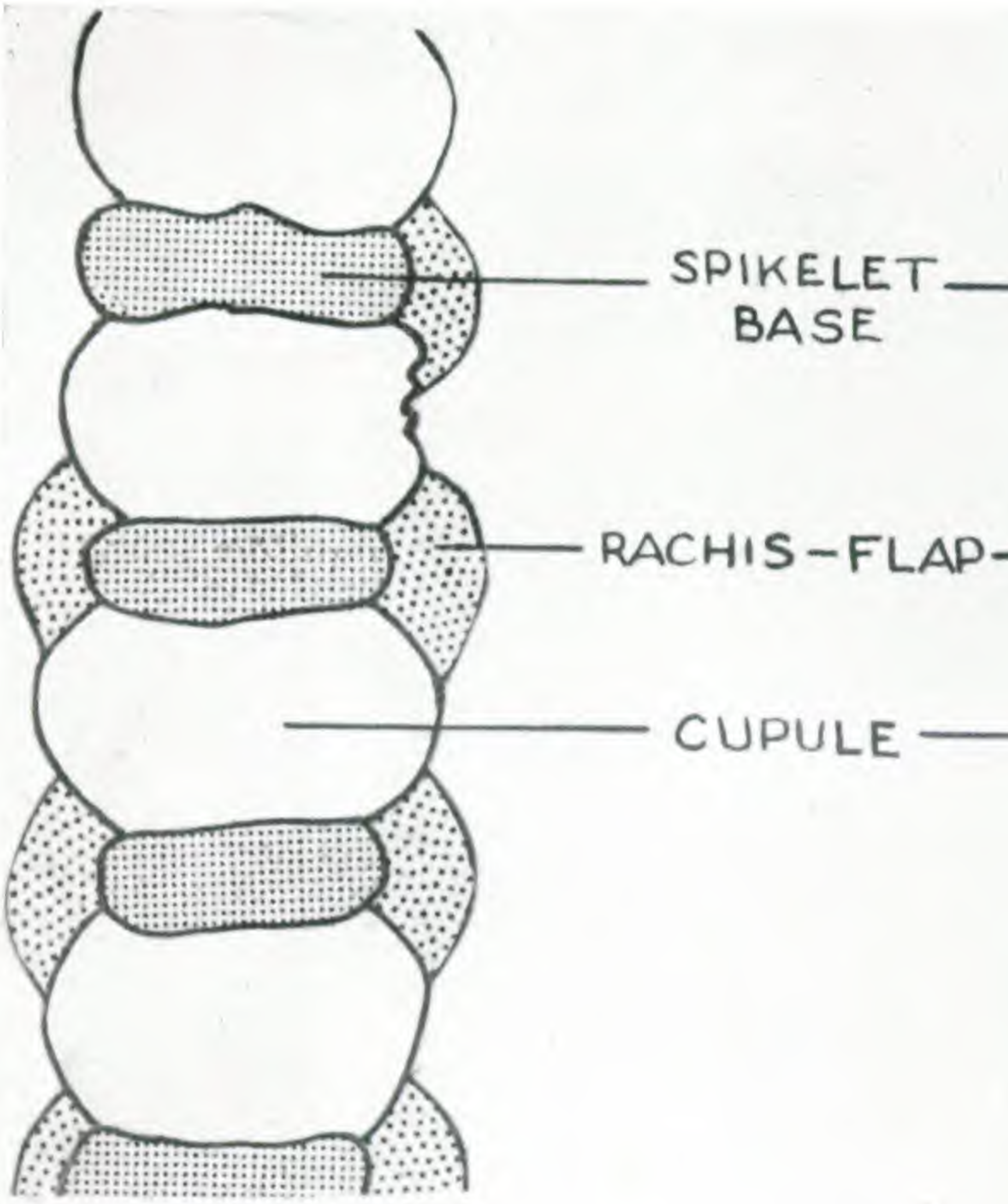
Fig. 4. Cupule with pedicel of spikelet pair rising out of it.

Fig. 5. Cupule with longitudinal section of pair of spikelets.

Fig. 6. Areas of dense sclerenchyma at either side of spikelets show the beginning of the cupules which will appear immediately above the spikelets shown in fig. 1.



LENZ—HISTOLOGY OF THE CORN COB



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LENZ—HISTOLOGY OF THE CORN COB

Explanation of Plate

PLATE 40

Figs. 1 and 2. Photograph and tracing of photograph of immature 4-rowed cob from F_1 plant of *Zea* × *Euchlaena* with spikelets dissected out.

Fig. 3. Six-rowed cob from F_1 plant of *Zea* × *Euchlaena*. This cob produced only a single spikelet on each cupule.

Fig. 4. Cross-section of the 4-rowed cob illustrated in fig. 2. Note size and shape of rachis-flap.

Explanation of Plate

PLATE 41

Serial series of longitudinal sections of Chiapas #81 (flexible cob), a variety with little sclerenchyma tissue.

Fig. 1. In a few places the vascular strands of the inner system can be seen. The small bundles of the section belong to the outer vascular system.

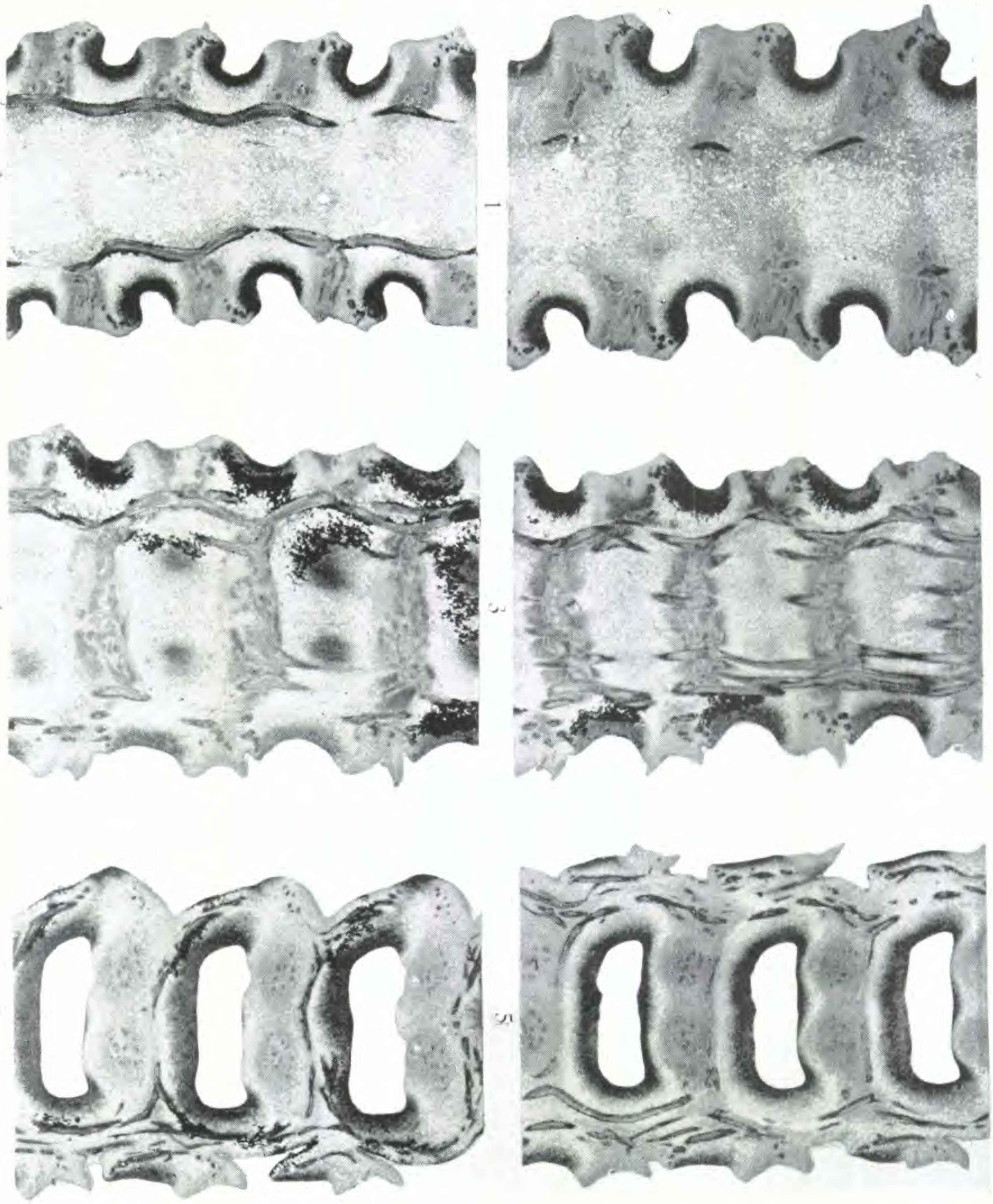
Fig. 2. Sclerenchyma surrounding cupules at side of section. The large vascular strands belong to the inner vascular system, and the small bundles between the large strands belong to the outer vascular system.

Fig. 3. Nodes of rachis show the anastomosing of the vascular strands which pass through the second node without branching.

Fig. 4. Nodes of rachis can be seen and at the sides the beginnings of the next cupules which will be at a 108° angle from the cupule shown in fig. 6.

Fig. 5. Strands of vascular tissue can be seen at side of cupule opening.

Fig. 6. Dark area above and to the sides of the opening of the cupule is heavy sclerenchyma. Gray circular areas below openings are vascular strands of the spikelet surrounding the branched sclerenchyma.



LENZ—HISTOLOGY OF THE CORN COB

THE ROLE OF POD CORN IN THE ORIGIN AND EVOLUTION OF MAIZE

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THE POD-CORN HYPOTHESIS

The hypothesis which holds that cultivated maize has been derived from a wild form of pod corn at one time indigenous to the lowlands of South America is at once the oldest and among the youngest of the various propositions which have been developed to explain the origin of this unique New World cereal. More than a century ago the French naturalist, Saint-Hilaire (1829), described as a new variety *Zea Maïs* var. *tunicata*, a peculiar type of maize sent to him from Brazil in which the grains were covered by the glumes. He concluded that this was the natural state of maize and that South America (Paraguay) was its native home. Virtually all students of maize since Saint-Hilaire have given serious attention to pod corn, have recognized its primitive characteristics, and have either accepted it as the ancestral form, or, for a variety of reasons, have dismissed it from this role. Their viewpoints and conclusions are reviewed and discussed in detail by Mangelsdorf and Reeves (1939). Here it will suffice to set forth the principal reasons given by various students who dismissed pod corn as the ancestral form of maize: (1) it does not breed true; (2) it apparently arises spontaneously in cultures of normal maize; (3) it is frequently monstrous; (4) it differs from normal maize primarily by a single gene; (5) the hypothesis that teosinte is the ancestral form of maize is a more plausible one.

Of the five reasons given for rejecting the pod-corn hypothesis the last is particularly important, for, once the close relationship of maize and teosinte was widely recognized, the pod-corn hypothesis was relegated to a distinctly secondary role. Only recently has it again been brought into prominence by Mangelsdorf and Reeves (1939) who, on the basis of experimental evidence, concluded that teosinte, far from being the progenitor of maize, is instead the progeny of the hybridization of maize and *Tripsacum*. Having dismissed teosinte as the ancestral form of maize, they turned to the earlier pod-corn hypothesis as the only plausible alternative.

The present paper is concerned not with the entire problem of the origin of maize but primarily with the pod-corn hypothesis, and particularly with a mass of new experimental evidence and new observations accumulated during the past ten years which have a bearing upon the problem of the role of pod corn in the origin and evolution of maize. Data previously published are included only to the extent that they are needed in presenting a complete picture; and the extensive literature on pod corn is reviewed only to the extent of providing an adequate background for the present discussion. For more detailed reviews of the literature on pod corn and for earlier data the reader is referred to Sturtevant (1899), Weatherwax (1935), and Mangelsdorf and Reeves (1939).

THE HISTORY AND DISTRIBUTION OF POD CORN

Early History References.—

Since the early history of pod corn has been adequately treated by Sturtevant (1899) there is no necessity for including a detailed review here, and only those references which appear to be highly significant to the pod-corn hypothesis are mentioned. The four references to pod corn which appeared in the first third of the nineteenth century seem to me to be especially important. These are: Azara (1809), Dobrizhoffer (1822), Saint-Hilaire (1829), and Bonafous (1836). All deal with pod corn in South America and three of them with pod corn in Paraguay. Two of them, significantly, speak of pod corn as *bisingallo* or *pinsingallo,* words undoubtedly related to the modern words *pisingallo, passankalla, pisincho, pisinga,* and *piksenkella* which Parodi (1935) and Granado (1931) have listed as being used in South America for varieties of pop corn. Mangelsdorf and Reeves (1939) have pointed out that the use of the word *pinsingallo* in connection with pod corn in the nineteenth century and the use of its derivatives in connection with pop corn in the twentieth century is quite consistent with the conclusion first clearly stated by Sturtevant (1894) that primitive corn was both a *pod* corn and a *pop* corn.

Experimental Verification of an Historical Reference.—

Especially significant to the pod-corn hypothesis and of particular interest in connection with the conclusion that primitive corn was both a pod corn and a pop corn is Azara's (1809) description of the fourth kind of maize which he encountered in Paraguay. Since this description has been quoted in full elsewhere (Mangelsdorf and Reeves, 1939), it need only be said here that Azara described a variety of maize bearing covered seeds in the tassel. This corn was utilized by heating the tassel in oil, whereupon the kernels, still attached to the tassel, exploded to produce, in Azara's own words, a "superb bouquet capable of adorning at night the head of a lady."

By crossing pod corn with pop corn and by backcrossing the hybrid to pop corn for several generations it has been possible to produce a corn which is both pod corn and pop corn and which dipped in hot oil behaves precisely like the fourth variety described by Azara. This simple experiment is not proof that Azara was describing a primitive form of corn. It does prove, however, that what he described *could* have been a pod-pop corn. And since the third variety of corn which Azara described was obviously pod corn there is little doubt in my mind that Azara has given us a description, remarkably picturesque and vivid, of a primitive homozygous pod corn whose seeds were not only covered but also were small, hard, and capable of popping.

Present Occurrence of Pod Corn.—

During the second two-thirds of the nineteenth century, pod corn was repeatedly reported from various parts of North America. It is difficult to determine the significance of some of those reports since pod corn came to be regarded as an interesting curiosity and was actually sold as a novelty by seedsmen (Sturtevant, 1899). Even today it is still passed from person to person and grown as a curiosity so that its occasional spontaneous appearance in open-pollinated fields is of no significance from the standpoint of proving recurrent mutation.

Much more significant, I think, is the possession of pod corn by native peoples. Parker (1910) stated that pod corn was among the varieties grown by the Mohawk and Iroquois Indians and that by the latter it was regarded as sacred. Pod corn occurs in Mexico. I have never encountered pod corn in the field in Mexico but Ing. Eduardo Limón and Ing. Edmundo Taboada of the Dirección de Agricultura in Mexico both have told me that pod corn exists in Mexico, and it has been reported by Khankhoje (1930). There are also ears of pod corn of uncertain origin on display in the local museum near the pyramid of Teotihuacán.

Pod corn is widely known in South America. Contrary to Cook's conclusion (cf. Collins, 1917) that pod corn is unknown in Peru and that there are no words for it in the Quichua vocabulary it can now be said that pod corn, although not common, is well known not only in Peru but also in Bolivia, Ecuador, and Colombia, and that there is a well-recognized term *paca sara* meaning "hidden maize" to describe it. Cutler (1944) has made several collections of pod corn in Bolivia and has made the interesting suggestion that it has been kept in existence and distributed far and wide by the Callahuayo itinerant medicine men. Pod corn of several distinct types, one of which is illustrated in pl. 43A, has been sent to me by Professor Cesar Vargas from Peru. Dr. Arthur G. Kevorkian has told me that pod corn is grown for its magical properties in Zamora, Ecuador, and Dr. Fernando Villamil of the Agricultural Experiment Station at Palmira, Colombia, has informed me that pod corn is well-known in several localities in Colombia. Brieger (1945) has described a form of pod corn from Brazil.

Pod Corn in Prehistoric Maize.—

There at least one authentic specimen of prehistoric pod corn in the Museum of Northern Arizona at Flagstaff, mentioned by Cutler (1944). The ears of pod corn in the Museum at Teotihuacán in Mexico, already mentioned above, are said to be prehistoric but the evidence is not conclusive. In addition, there are a number of prehistoric ceramic replicas of corn ears which *may* represent pod corn. One of the most convincing is the specimen in the Peabody Museum of Yale University illustrated by Mangelsdorf and Reeves in their fig. 92. Another from the same museum which may be, but certainly is not necessarily, pod corn is illustrated in their fig. 15. Several of the representations of maize on early Peruvian pottery at the American Museum of Natural History show at least external resemblances to pod corn (Mangelsdorf and Reeves, fig. 16). Finally there is a specimen in

the Museum of the University of Pennsylvania which might easily be taken as representing pod corn.

The probability that some or all of these prehistoric specimens were intended to represent pod corn has been enormously increased by the discovery, described elsewhere in this paper, that many of the actual ears of prehistoric corn still in existence are a weak form of pod corn.

THE NATURE OF POD CORN

Genetic Nature.—

Genetically, pod corn, or "tunicate" as it is commonly known among maize geneticists, is the phenotypic expression of a single gene *Tu* located in the long arm of chromosome 4. The *Tu* gene is strongly but not wholly dominant. It always manifests itself in the heterozygous condition but two doses of the gene usually produce a greater effect than one. The *Tu* gene is responsible for producing the principal effects which are characteristic of pod corn, but the degree to which these effects manifest themselves is strongly influenced by modifier factors which are undoubtedly distributed over several chromosomes and probably over the entire chromosome complex.

Morphological Nature.—

The expression of the *Tu* gene varies with the environment and with the background of modifying factors, but the gene is one which usually has manifold effects. Those most commonly recognized are described below:

Glumes:—The principal characteristic of pod corn is that the glumes, which in ordinary corn are reduced to inconspicuous bracts, are completely functional and, as in other cereals, enclose the caryopsis. There is enormous variation in the degree to which the glumes develop. In some ears they are monstrous; in others they scarcely enclose the grain. On any one ear of pod corn the glumes are usually more strongly developed at the base of the ear than at the tip. The reason for this is not known.

The *Tu* gene affects not only the glumes of the pistillate spikelets but also the glumes of the staminate spikelets in the tassel. This second effect is less noticeable than the first since the staminate spikelets already normally have glumes completely enclosing the floral structures. Nevertheless, it is usually possible to distinguish tunicate or heterozygous tunicate plants from non-tunicate plants in the same family by the size of the glumes on the staminate spikelets.

Another characteristic of the glumes of pod corn is that they are membranaceous or papery rather than indurated or horny. In this respect pod corn differs not only from teosinte and *Tripsacum*, the closest relatives of maize, but also from most varieties of *Coix* and of *Sorghum*. Membranaceous glumes are not, however, unique to pod corn since they are characteristic of many grasses.

Staminate and Pistillate Spikelets:—The second most conspicuous effect of the *Tu* gene is evident in the terminal inflorescence or tassel. This structure, normally

wholly staminate in the majority of modern corn varieties, becomes partly pistillate in the presence of the *Tu* gene, sometimes in plants heterozygous for the gene, almost always in plants homozygous for it.

The transformation of a staminate inflorescence to a partly pistillate one may occur in various ways. Dissection and examination of several thousand florets in the tassels of *TuTu* and *Tutu* plants have led to the following observations:

1. Florets on a mixed inflorescence may be: (a) functionally pistillate; (b) functionally staminate; (c) perfect; (d) functionally pistillate with visible but non-functional anthers; and (e) abortively staminate.

2. Pistillate or perfect florets are most common in the lower spikelets on the tassel branch, but are not confined to them.

3. If both florets in a single spikelet develop, both may be staminate (common), both pistillate (rare), the upper pistillate and the lower staminate (rare), or the upper perfect and the lower pistillate (common).

4. If only one floret in a spikelet is pistillate, it is invariably the upper.

5. If only one floret in a spikelet is perfect, it is invariably the upper.

6. When pistillate, perfect-flowered and staminate spikelets all are found on the same branch, the pistillate are likely to occur below, the staminate above, and the perfect-flowered between.

The degree to which the tassels of pod corn become pistillate, like the development of the glumes, varies with the environment and the genetic background. There is, however, a strong correlation between glume development and sex-reversal in the tassel. Heterozygous tunicate plants which are strongly pistillate in the tassel are almost certain to have prominent development of glumes on the ear, when there is an ear.

If the terminal inflorescence, or tassel, is strongly pistillate, then the lateral inflorescence, or ear, is likely to be suppressed. This is probably a simple matter of the amount of plant nutrients available, and the fact that the terminal inflorescence apparently has priority in its requirements. It is usually possible to induce the formation of an ear in a tunicate plant which would otherwise be earless by removing the tassel soon after it emerges.

Secondary Pistillate Florets:—The tunicate condition is often, but by no means always, accompanied by the development of secondary pistillate florets. This may occur either in the tassel or in the ear. An example of the latter is illustrated in pl. 45C. This condition, which is a genetic one in the sweet corn variety, Country Gentleman, is in tunicate maize undoubtedly the consequence, at least in part, of the release which the tunicate condition provides from compaction and pressure. This is suggested by ears which have elongated beyond their husks. On such ears, spikelets with the lower floret developed occur almost invariably in the region not compressed by the husks.

Branching of the Ear:—In some stocks, notably in my crosses of pod corn with the Guarany maize of Paraguay, the tunicate condition is often accompanied

by basal branching of the ear. Since the basal branches are two-ranked, they contribute toward producing a structure which, except for the fact that it is pistillate rather than staminate, is the exact counterpart of the tassel, a polystichous central spike with distichous basal branches. An ear of this type is shown in pl. 44.

Basal branching of the ear, like the development of secondary florets, is probably in part a response to release from compaction.

Elongation of the Rachis:—One of the most conspicuous effects of the tunicate gene, and one whose consequences have already been described in part, is a release of the strong compaction characteristic of the normal modern ear of corn, which, as I have pointed out elsewhere (1945), is a strongly compacted structure. The extent to which compaction is released, like other effects of the *Tu* gene, varies with the environment and with the genetic background. In some stocks, again notably in crosses of pod corn by Guarany maize, the ear grows far beyond the husks and becomes so lax that its true nature is clearly revealed (pl. 42). The rachis is slender and fragile like the rachises of other cereals. The paired nature of the pistillate spikelets, obscured in many modern varieties of maize, is readily apparent, and in some cases the sessile and pedicellate members of the pair are distinguishable. In some ears of pod corn the whorled phyllotaxy of the inflorescence is also clearly revealed.

Elongation of the "Shank":—Also, sometimes, but by no means always, accompanying the tunicate condition is an elongation of the stalk, commonly known as the "shank," upon which the ear is borne. Here again environment and modifying factors play a part. The most striking example of this elongation which I have encountered occurred in a plant of Guarany pod corn which bore three ears on its main stalk and one ear on each of its three tillers. The ears on the tiller stalks were normal with contracted shanks and normal husk covering, but the three ears on the main stalk all had elongated shanks bearing more or less normal leaves instead of husks at the nodes, and terminating in naked or partly naked ears. This plant is an excellent demonstration of the widely accepted conclusion that the ear of maize is the terminal inflorescence of a lateral branch which has become drastically contracted and that the husks are leaf sheaths arising from each node which have largely lost their leaf blades and which because of the contraction of the branch have become strongly overlapping. This plant also demonstrates that all of these profound changes can occur spontaneously and almost as a single step. In this instance the tunicate gene has apparently brought the plant to a threshold where slight differences in the environment (the kind of difference in environment which exists between the main stalk and the tillers) may have drastic and dramatic effects.

Other Effects: How many other effects the *Tu* gene produces remains to be determined. Preliminary investigations by Prat (reported in a conversation)

indicate that the epidermal characteristics of tunicate maize are different from those of non-tunicate maize and are of a category which he regards as primitive for the grasses. There is little doubt that still other differences between tunicate and non-tunicate maize will be found when more intensive morphological studies have been made.

Effect of Tu on Teosinte.—

Brieger (1944) is of the opinion that the spikes resulting from crossing teosinte and pod corn followed by backcrossing to teosinte provide an experimental reconstruction of wild corn. I do not share that opinion. It is clear, however, that such crosses can shed light not only on the morphological nature of teosinte but also on that of pod corn.

Certain effects of pod corn are emphasized and clearly revealed when the *Tu* gene is introduced into varieties of teosinte by hybridization of pod corn and teosinte, followed by repeated backcrossing to teosinte. Fruits of tunicate teosinte compared with fruits of normal teosinte are illustrated in pl. 46. In normal teosinte the fruit case comprises an indurated glume of restricted proportions plus an indurated rachis segment which internally is concave and partly surrounds the caryopsis. In tunicate teosinte the caryopsis is completely enclosed by prominent, membranaceous glumes, and the rachis segment becomes nothing more than an appendage[1], playing no part in enclosing the caryopsis. These two fruit cases, so different that if encountered in nature they would undoubtedly be assigned to different species if not to different genera, are the products of the two genes *tu* and *Tu*. The segregation of the two types is approximately 1:1 in backcrosses of the heterozygote to the recessive. This fact may be of considerable significance in the study of the world's corn varieties. It is almost certain that varieties of corn originating from a strong introgression of *Tripsacum* into maize, either directly or through contamination of maize by teosinte, would have quite a different cob anatomy from those originating directly from any kind of tunicate maize. The former, which we may call "tripsacoid," would be a compound structure made up of individual units fundamentally like the fruit case of normal teosinte, but modified by crowding and pressure. Such a cob would be expected to have a thick, stiff, and indurated rachis with distinct rachis cavities from which arise spikelets whose outer glume is reduced to an indurated bract. On the other hand, a cob derived from a tunicate or weak tunicate maize, which we may call "tunicoid," would be expected, since it is made up of units fundamentally like the fruit case of tunicate teosinte, to have a slender, flexible, or fragile rachis, with the spikelets arising from its surfaces partly enclosed in membranaceous glumes.

There is no doubt that maize varieties possessing these two kinds of cobs exist. And since stocks with the indurated rachis and glumes of teosinte can be produced by controlled introgression of teosinte into maize there is little doubt that some

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[1]None of the fruits of tunicate teosinte in my cultures resemble those illustrated by Brieger in which the rachis remains intact and separation occurs at the base of the grain.

maize varieties of this type have arisen through such introgression. On the other hand, since the two types of teosinte described above differ primarily by a single gene it is possible that a tripsacoid type of maize ear, or something approaching it, can result from a simple mutation of *Tu* or one of its alleles to *tu* in a tunicoid type.

Most of this is obviously highly speculative and is included here only because it suggests some of the problems to which pod corn seems to hold at least one of the keys.

The Primitive Nature of Pod Corn.—

Many, if not all, of the effects of the *Tu* gene result in conditions which have been recognized as primitive by students of maize and its relatives. That wild corn must have had its grains enclosed in glumes has been noted by virtually all students of maize. That the ear is the terminal inflorescence of a drastically contracted lateral branch is widely accepted. That the husks are overlapping leaf sheaths minus the leaf blades is scarcely a matter for dispute. That the ear is the counterpart of the central spike of the tassel and is similar to a tassel minus its basal branches has been pointed out by several writers. Hence, in all of these features the *Tu* gene has the *tendency* to restore a condition which was undoubtedly characteristic of primitive maize.

It is possible, but not certain, that the tendency of tunicate maize to develop perfect-flowered spikelets and secondary pistillate florets also represents a reversion to a more primitive condition. It is generally recognized that the remote ancestor of maize and its relatives must have been perfect-flowered. But since *Tripsacum* and teosinte, the closest relatives of maize, are monoecious rather than perfect-flowered, I am inclined to believe that the occurrence of perfect-flowered spikelets in the tassels of tunicate maize represents a transition from a wholly staminate condition to one in which, as in *Tripsacum*, there are staminate and pistillate spikelets borne more or less separately on the same branches. The evidence for this, in so far as there is any evidence in tunicate maize, lies in the fact that inflorescences which are wholly perfect-flowered are never found. Perfect florets occur only in mixed inflorescences and are often found between a part of the branch bearing mainly pistillate florets and one bearing mainly staminate florets.

The significance of secondary pistillate florets in pod corn is even less clear. As already suggested, they may be nothing more than the consequence of a release from compaction. On the other hand, since the development of both florets is undoubtedly primitive in the grasses and since there are varieties of maize such as Country Gentleman in which the development of both florets is the rule rather than the exception, I suspect, although I certainly cannot prove, that the development of both florets in pod corn represents a tendency to revert to a condition characteristic of primitive maize. In this connection it is of interest to note that Dr. Cutler collected in the same village in Bolivia ears of tunicate maize and ears of maize which were not only branched but also bore secondary pistillate florets.

Leaving open the question of the significance of perfect florets and secondary pistillate florets in pod corn it is still obvious that the *Tu* gene is one which has a tendency to restore, not only the universally recognized primitive characteristic of glume-covered seeds, but an entire complex of primitive characteristics as well.

NEW GENETIC EVIDENCE ON POD CORN

True-breeding Pod Corn.—

One of the recurrent objections to the pod-corn hypothesis is that pod corn does not breed true. Homozygous pod corn, when it occurs in the cultures of the geneticist, is usually pollen-sterile and hence incapable of reproducing itself. It has already been pointed out (Mangelsdorf and Reeves, 1939) that this objection is not necessarily valid, since, if pod corn were the primitive type, then the *Tu* gene of today is a relict "wild" gene superimposed upon a genetic background frequently lacking in the background of modifiers which once kept the character under control. In the absence of these controlling modifiers the tunicate character would be expected to result frequently in monstrous development of the glumes accompanied by partial or complete sterility. This sterility is sometimes structural and sometimes probably physiological. Structural sterility exists when functional anthers are formed which, because of the sheer massiveness of the glumes surrounding them, are incapable of becoming exserted. Sterility thought to be of a physiological nature occurs when the glumes are so monstrous and demand so much energy in their development that, as a result, both male and female reproductive organs are abortive. In any case, there is great variation in the development of the tunicate character, and, as I previously pointed out (1947), there seemed to be a possibility of producing a completely fertile form of pod corn either by (a) selecting for restraining modifying factors or (b) substituting for the modifier complex of present-day pod corn a more ancient complex obtained from a primitive variety.

In a previous paper (1947) I reported that an experiment involving selection for minus modifiers of pod corn had been brought to a successful conclusion. I must now modify that statement, for although I did succeed in producing a number of true-breeding lines of pod corn by selection for minus modifiers, the extreme form which I described and illustrated has since proved to be the product not only of the accumulation of minus modifiers but also of a new allele at the *Tu-tu* locus. This new form of pod corn is described in some detail later in this paper. Homozygous forms of pod corn involving the original allele have much more prominent glumes than the new form illustrated in my previous paper (1947).

The other experiment previously reported, which sought to develop a true-breeding pod corn by introducing the modifier complex of a primitive variety, has not yet been completed. There is no doubt that the Guarany maize from Paraguay which was used in this experiment possesses modifiers capable of restraining the tunicate character. Furthermore, homozygous tunicate plants derived from

this experiment which are both male-fertile and female-fertile have been observed. There is little doubt, therefore, that a homozygous true-breeding form of pod corn will be produced in due time as a consequence of introducing modifiers of the tunicate character from a primitive variety.

Alleles of Pod Corn.—

As already mentioned, the attempt to produce a true-breeding pod corn through selection for minus modifiers resulted in the discovery of a new allele of *Tu*. The circumstances were as follows: in 1942, in a population derived from self-pollinating a *Tutu* plant during the previous season, one plant was found which not only appeared to be homozygous tunicate, bearing pistillate spikelets in the tassel in profusion, but was also male-fertile. This plant was self-pollinated in the tassel and gave rise in the following generation, which was grown in 1944, to a population of 64 plants, all of which were tunicate. A number of these were self-pollinated and in addition were crossed on various inbred strains, primarily A158 and P39, in order to provide a final test for homozygosity for *Tu*. The crosses thus produced were grown in the season of 1945. Some of these F_1 crosses were so weakly tunicate that they appeared at first glance to be non-tunicate. This weakly tunicate condition was thought at the time to have been the consequence of selection for minus modifiers, but it has since become apparent that the new pod corn involves not only minus modifiers but a new allele of *Tu* which has apparently arisen spontaneously in the course of these experiments. The existence of this allele was first indicated when one of the crosses made to test homozygosity gave rise to strongly tunicate and weakly tunicate plants in a ratio of 8 to 5. The results were verified by repeating a planting of the same cross in 1946 when 10 strongly tunicate and 15 weakly tunicate plants were counted. A third planting in 1947 yielded the two types in a ratio of 8 to 4. The ratio in the total population is 26 strongly tunicate and 24 weakly tunicate. Obviously, the plant selfed in 1944 which furnished the pollen of this cross was either heterozygous for two alleles of *Tu* or was segregating for a major modifier of this gene. The first explanation is now known to be the correct one. Since the weaker form of tunicate produces approximately the same effect when homozygous as does the stronger when heterozygous, it may appropriately be designated as "half-tunicate," and assigned the symbol tu^h. It is illustrated in pl. 47.

Since this cross had been made on the inbred P39 which is pure for sugary, a gene on the fourth chromosome, a further test for allelism was easily made by backcrossing the hybrid to a sugary stock. Plants of two such backcrosses, one with a tunicate hybrid as one parent, the other with a half-tunicate parent, were grown in the summer of 1948 with the following results. The backcross of sugary to the strongly tunicate hybrid yielded four classes in the numbers shown:

Starchy tunicate	32	
Starchy non-tunicate	14	37 crossovers = 38 per cent
Sugary tunicate	23	
Sugary non-tunicate	29	

The backcross of sugary to the heterozygous half-tunicate yielded four classes in the following numbers:

Starchy half-tunicate	34	
Starchy non-tunicate	16	28 crossovers = 30 per cent
Sugary half-tunicate	12	
Sugary non-tunicate	32	

The results are in harmony with the assumption that the strong and weak forms of tunicate are due to different alleles of *Tu*.

Are There Modern Varieties of Pod Corn?—

Once it was suspected that half-tunicate is an allele of tunicate, the questions at once arose: Are there still weaker alleles of *Tu*? And are there modern varieties of maize which are in reality weak forms of pod corn? An examination of the ears in my collection indicated at once that there are living varieties which give the impression of being weak pod corn. The cobs are flexible and the caryopses are partly covered by membranaceous glumes. In some varieties these glumes are sufficiently developed to almost enclose the seeds, particularly toward the base of the ear where the glumes of pod corn are, as already mentioned, usually most prominent.

The assumption that these types are actually weak forms of pod corn is verified by linkage data. In 1947, for example, there was available in my cultures a population of plants resulting from a cross of a Guatemalan variety, No. 16, with the sweet corn variety, Country Gentleman. The cross had been made to study the linkage relations of pilosity, and the starchy and sugary seeds had been planted separately. When it was discovered that the variety Guatemala 16 appeared to be a weak form of pod corn, a classification of weak-tunicate and non-tunicate was attempted. The difference between them was manifested more strongly in the stiffness and flexibility of the cob than in the glumes themselves. Two classifications, one made by the writer and the other made completely objectively by an assistant who, unaware of the problem involved, merely classified the ears as stiff or flexible, yielded the following results:

	Classified by PCM	*Classified by LMJ*
Starchy; flexible	18	21
Starchy; stiff	9	6
Sugary; flexible	6	12
Sugary; stiff	25	19
	58	58

In spite of the discrepancies, there is in both classifications a definite association between starchy endosperm and flexible cobs and sugary endosperm and stiff cobs. If we suppose that flexibility represents one manifestation of a weak form of tunicate, which we may designate as tu^{w}, then the two middle classes above represent crossovers between *Su* and tu^{w} and *su* and *tu*. In the first classification these comprise 26 per cent of the total; in the second, 31 per cent. Both figures are remarkably close to the 29 per cent of crossing over which normally occurs between *Su* and *Tu*. We have, therefore, a strong indication that the flexibility which is characteristic of the cob of Guatemala No. 16 is actually a weak form of tunicate.

Two additional backcross populations of this type, one involving a Guatemalan and the other a Nicaraguan variety, were grown in 1948. Distinct variation occurred in both populations but was more apparent in the fragility of the cob than in its flexibility, perhaps because the ears had been more completely dried than those grown in 1947. In any case, it was possible to separate the ears into two distinct classes, fragile and solid, on the basis of the ease with which the cobs were snapped in two. The results of such a classification are as follows:

	Family 1583	Family 1585	Total
Starchy; fragile	33	31	64
Starchy; solid	12	15	27
Sugary; fragile	18	12	30
Sugary; solid	25	31	56
	88	89	177

If we assume that fragility of the cob is due to a weak tunicate allele of tu^{w} then the two middle classes, starchy; solid, and sugary; fragile, represent crossovers. These comprise 32 per cent of the total. Considering the small size of the sample, this is remarkably close to the approximately 29 per cent expected if fragility is the result of a weak allele of *Tu*.

These combined data strongly indicate that the three varieties involved in these crosses were weak-tunicate and they also indicate that the gene for this condition has its locus on the fourth chromosome approximately 30 crossover units from *Su*, exactly where an allele of *Tu* would necessarily have its locus.

Genetic Tests for Alleles of Tu.—

A corollary of the assumption that fertile forms of pod corn can be produced by introducing controlling modifiers from primitive varieties is that the farther removed a variety becomes from its center of origin and its original pod-corn ancestor, the fewer controlling modifiers it will have retained. Hence, if maize originated from a wild pod corn once indigenous to the lowlands of South America, we should expect to find controlling modifiers of pod corn in highest frequency in South American varieties and in lowest frequency in the United States.

To test this assumption, 116 varieties and inbred strains of corn from eight

Latin American countries and from various regions of the United States were crossed on a uniform inbred strain of half-tunicate. The ears of the F_1 hybrids were then studied and classified with respect to the development of the tunicate condition. There was, as expected, considerable variation in the development of the glumes in the F_1 hybrids ranging from those in which the glumes were not visible unless the grains were removed, to those in which the glumes completely covered the seed. The ears were arbitrarily divided into four classes on the basis of a "glume score" defined as follows:

Glume Score	*Definition*
1	Glumes scarcely apparent.
2	Glumes apparent but do not cover grains.
3	Glumes cover grains on lower part of ear.
4	Glumes cover practically all grains.

When these glume scores were averaged for different countries, and for different areas of the United States (cf. Table I), there proved to be, as had been anticipated, consistent regional differences. But the results were *exactly the reverse* of those predicted. Crosses with South American varieties which were expected to have the lowest glume scores because of controlling modifiers of the tunicate condition had the highest glume score, while varieties from the United States, expected to be highest in glume score, were lowest.

TABLE I

AVERAGE "GLUME SCORES" IN F_1 HYBRIDS OF MAIZE VARIETIES AND INBRED STRAINS WITH AN INBRED STRAIN OF POD CORN

Country, State, or Group	Number of varieties	Glume score
Paraguay	3	3.7
Bolivia	3	3.3
Brazil	2	2.0
Nicaragua	3	3.0
Costa Rica	1	3.0
Mexico	35	2.9
Cuba	3	2.8
Guatemala	6	3.4
Texas	9	2.2
North Carolina	6	2.8
Corn-Belt	17	1.5
Minnesota	10	1.8
Wisconsin	5	2.0
U. S. Sweet Corn Varieties	13	2.1
Av. South America	8	3.1
Av. Central America & West Indies	48	2.9
Av. United States	60	2.0

When an experiment, as in this case, yields results exactly the reverse of those anticipated, it does not mean that the experiment is a failure or that the inductive reasoning which led to it is entirely fallacious. On the contrary, the fact that an experiment yields conclusive results, even if in the "wrong" direction, indicates that the basic premise upon which it rests must have some validity. In this case, the basic premise that South American and North American maize varieties differ in their ultimate relationship to pod corn is undoubtedly valid. But the assumption that this difference is primarily one of modifiers affecting the tunicate conditions is not established. Undoubtedly there are modifiers affecting the tunicate condition; indeed, this fact is easily demonstrated. Perhaps it is even true that controlling modifiers of tunicate have a higher frequency on the average in South American varieties than in North American, but if so, the fact is not established by this particular experiment. What this experiment demonstrates, I think, is that South American and North American varieties of maize differ primarily not in modifiers of tunicate, but in weak alleles of tunicate. When the inbred strain of half-tunicate, tu^h, is crossed with a variety homozygous for weak tunicate, tu^w, then the F_1, $tu^h tu^w$, might well be expected to have stronger glumes than an F_1, $tu^h tu$, resulting from a cross with a non-tunicate variety *tu*.

On this assumption the results in Table I become completely intelligible in terms of the pod-corn hypothesis and are completely in harmony with it. South American varieties have the highest average glume score presumably because weak alleles of *Tu* have their highest feequency in South America. Central American varieties are intermediate in glume score, and United States varieties lowest. Within the United States the strains of the Corn-Belt proper have lower glume scores than those of any other part of the United States.

The regional differences in glume scores of these F_1 hybrids is strongly correlated with the morphological appearance of the cobs of the parental varieties. The frequency of cobs with "pockets" and the alveolate appearance characteristic of weak pod corn is high in Paraguay, Bolivia, Peru, Ecuador, Colombia[1], Costa Rica, and Guatemala. It is less high in Mexico and the West Indies, and is lowest in the inbred strains of the Corn Belt of the United States. Ears with alveolate cobs from Peru, Colombia, and Mexico are compared with an ear known to be heterozygous for half-tunicate in pl. 48.

The correlation is by no means complete, however, for two varieties which are identical in appearance with respect to the development of glumes may produce quite different hybrids when crossed with tunicate. Furthermore, two varieties whose hybrids with tunicate are identical in glume score may themselves be quite different in appearance. These discrepancies can be attributed to modifier

[1] So far as external appearance alone is concerned weak pod corn seems to have its highest frequency in Colombia. This is the only new evidence which I have encountered which supports the conclusion of Birket-Smith (1943) that maize had its origin in Colombia. Cutler (in press) has criticized the linguistic evidence on which Birket-Smith's conclusion is largely based but the evidence from pod corn lends new significance to it. The question of whether maize originated in the Paraguay-Bolivia region or in Colombia is still open but the conclusion that it originated in South America has become almost a certainty.

complexes superimposed upon allelic differences. There is little doubt that both are operating.

But whether the regional differences revealed by this experiment are the result of differences in tunicate alleles, in modifier complexes, or in both, the fact remains that there are consistent differences. This is itself highly significant with respect to the pod-corn hypothesis, for if pod corn is not an ancestral form, if it is simply a mutant which has arisen spontaneously again and again in the history of maize under domestication, then there is no reason why "clines" with respect to genetic factors affecting its expression should exist. The very fact that there are such clines is a strong indication that pod corn has had a role in the evolution of maize.

Additional evidence that both modifiers and alleles of *Tu* are involved in Latin American maize varieties can be obtained by backcrossing to the parental strain of half-tunicate their F_1 hybrids with half-tunicate. If a Latin American variety is *tutu*, then the F_1 hybrid is $tu^h tu$ and the backcross to half-tunicate, $tu^h tu^h$, should yield two genotypes, $tu^h tu^h$ and $tu^h tu$, in equal numbers. These two genotypes should be readily distinguishable but if modifiers are involved there should be noticeable variation within each class. On the other hand, if a Latin American variety being tested is weak tunicate, $tu^w tu^w$, then the two classes in the backcross are $tu^h tu^h$ and $tu^h tu^w$. These should be less easily distinguishable than the two classes expected in the first instance, and, if modifying factors are also involved, the variation within each class might well result in an overlapping of the two classes to the extent that the two genotypes cannot be accurately separated.

Populations from eight backcrosses have been grown involving two varieties each from Mexico and Nicaragua and four from Guatemala. Four of these yielded two distinct classes with marked variation in each class but with no overlapping. In the remaining four, distinct classes did not occur. There was marked variation in the development of the glumes but it was not possible to separate the ears with complete accuracy into two distinct classes. It seems reasonable to conclude that modifiers of *Tu* were involved in all crosses but that the Latin American varieties entering into the first four crosses were of the genotype *tutu* while in the last four crosses they were $tu^w tu^w$.

MUTABILITY OF *TU* AND ITS ALLELES

As already mentioned, the weak allele of *Tu* now designated as half-tunicate, tu^h, occurred spontaneously in my cultures involving *Tu*. Since the total number of tunicate plants grown in cultures in which mutations could be detected did not exceed several hundred, it is obvious that *Tu* is either a mutable gene or the sample represented by my cultures is not a random one. Other data are available to indicate that the first explanation is at least in part the correct one.

In the fall of 1946, when harvesting ear-rows of a stock developed originally by crossing pod corn with the Guarany maize of Paraguay and backcrossing repeatedly to the Guarany variety, I discovered one ear heterozygous for *Tu* which was a chimera with respect to the tunicate and non-tunicate condition. Approxi-

mately three-fourths of the ear bore seeds enclosed in glumes while the remainder, comprising one side and the entire tip of the ear, bore naked or partly naked seeds. The ear is illustrated in pl. 45A. Seeds from the two portions were planted separately in 1947 with the results shown below. The ear found in 1946 was open-pollinated so that outcrosses occurred in the progeny. These could, however, be distinguished from plants resulting from selfing or sibbing. The distribution of the progeny from the two portions of the same ear is as follows:

	Outcrosses		*Selfs or Sibs*		
	Tutu	*tutu*	*TuTu*	*Tutu*	*tutu*
Tunicate portion	0	3	4	3	1
Non-tunicate portion	0	4	0	2	4

The data, though not extensive, prove that the parent ear was heterozygous for *Tu*, and they strongly indicate that the ear was also a chimera with respect to the two kinds of somatic tissue *Tutu* and *tutu*. The indications are twofold. First, all of the outcrosses, seven in number, proved to be *tutu*. Had the parent ear been of the composition *Tutu* throughout, then the outcrosses should have comprised genotypes *Tutu* and *tutu* in equal numbers. The odds against all being *tutu* are 127:1. Secondly, the distribution of the three genotypes among the selfs and sibs is almost, though not quite, significantly different in the progenies from the two portions of the ear. Both of these facts are in harmony with the assumption that the parent ear was a chimera of *Tutu* and *tutu* tissue, and combined they lend a high degree of plausibility to that assumption. If this is indeed the case, then this represents a second mutation from *Tu*, this time to the allele *tu*, which has occurred in my cultures in the past ten years.

A controlled experiment on mutability involving the allele tu^h rather than *Tu* was conducted in 1947 and 1948. Plants of the inbred strain Minn. A158 were crossed by an inbred strain homozygous for two dominant genes, tu^h and *B*, the latter a gene responsible for sun-red plant color. Mutations could be readily distinguished in the progeny from the products of accidental contamination by the fact that the latter were recessive for both genes while mutations were recessive for only one. No mutations occurred in the *B* factor in a population of 2125 plants resulting from this cross while one non-tunicate sun-red plant was found. If this proves, on the basis of a progeny test, to be a mutation and not a phenocopy, then the mutation rate at the tu^h locus as determined by this single sample is 471 per million gametes. This is only slightly less than the rate, 492 per million, which Stadler found at the *R* locus.

So far as I know, the reverse mutation from *tu* to *Tu* has never been observed. True, tunicate plants for which a spontaneous origin has been assumed have sometimes been discovered in ordinary corn fields. Sturtevant (1894) and Sconce (1912) have both reported the appearance of pod corn in non-podded varieties but the circumstances do not rule out contamination in the previous generation, especially since pod corn has been widely grown as a curiosity. On the other hand, millions of ears of inbred strains and single-crosses have been grown in con-

nection with the production of hybrid seed corn in the past twenty-five years and not a single instance of the spontaneous occurrence of pod corn in these pedigreed cultures has been reported,[1] although other mutations, especially to teopod, have been encountered repeatedly. So far as these data are a criterion, they indicate that *Tu* is not a gene which arose recently through spontaneous mutation but is an ancient gene which has survived in the population perhaps for thousands of generations.

THE APPARENT SPONTANEOUS OCCURRENCE OF SOLITARY TUNICATE SPIKELETS

An interesting phenomenon which must certainly have often been observed, but which so far as I know, has never been reported, is the occurrence of one or more solitary tunicate spikelets or pairs of spikelets on ears which are apparently in all other respects non-tunicate. I have now encountered this phenomenon in three separate instances, in a Nicaraguan variety, in a Mexican variety collected by Dr. E. J. Wellhausen, and in an F_1 hybrid of Midget $\times$ P39. In the last case five different ears each bearing one or more tunicate spikelets were found in a population of 39 ears.

In addition to these three cases, I have received from Dr. Isabel Kelly of Mexico, through the kindness of Dr. Edgar Anderson, a single tunicate kernel found on an ear of Mexican maize. Dr. Kelly writes that kernels of this kind are occasionally found and that they are regarded as having magical properties.

All of these instances of the apparent spontaneous occurrence of tunicate spikelets can, I think, be explained as the monstrous development of glumes on weak forms of pod corn. Certainly this is true of the three ears which I encountered, and since weak pod corn is common in Mexico, I have no doubt that it is true of the case reported by Dr. Kelly. Why an occasional spikelet of weak pod corn should suddenly develop strongly tunicate and even monstrous glumes, and why such spikelets are always basal, is not clear. It is a fact, already mentioned, that the glumes of pod corn are usually more strongly developed on the lower spikelets of the ear than on the upper. It is also a fact that strains of half-tunicate corn sometimes develop monstrous glumes on basal spikelets. But whatever the reason for their occurrence the fact that they do occur is convincing visual evidence that weak forms of pod corn are still truly pod corn.

EVIDENCE OF WEAK POD CORN IN PREHISTORIC TIMES

Many of the prehistoric ears of corn from Peru which I have had an opportunity to examine exhibit the alveolate appearance and the deep "pockets" characteristic of the cobs of weak forms of pod corn. Furthermore, their frequency is highest among the ears from the more ancient sites. Two ears from Tello's Paracas collection are illustrated in pl. 45B, and one from his Nazca collection in pl. 48A. There is little doubt, I think, that all represent weak forms of pod corn.

[1] It is possible that ears of pod corn which occur in commercial fields are discarded at processing plants without being reported, but Mr. Ralph Gunn and Mr. R. R. St. John of the DeKalb Agricultural Association have both told me that they have never seen an ear of pod corn in their experimental hybrids. Each has approximately a half-million plants in his tests annually.

A comprehensive study of the prehistoric maize of the Southwest with respect to the presence of weak pod corn has not yet been made. I can only say that many of the ears in the collections of the Peabody Museum of Harvard University have cobs with strongly alveolate surfaces. Also, four ears recently discovered by C. T. Hurst at Cottonwood Cave, Colorado, and sent to me by him for examination have alveolate cobs which closely resemble not only the weak pod corn of modern varieties but also the prehistoric corn of Peru. Dr. Edgar Anderson has kindly given me permission to state here that of twenty-six ears of Basketmaker I corn in the museum at Mesa Verde National Park which were examined by him, eight had prominent glumes. There is little doubt that much, if not most, of the prehistoric corn of both North and South America is weak pod corn.

The facts (1) that the familiar form of pod corn has been found among prehistoric ears; (2) that it, or something curiously like it, is represented in prehistoric ceramic replicas; and (3) that many of the well-preserved ears of prehistoric corn from North and South America are identical in the structure of their glumes and in the alveolate condition of the cobs to modern forms of weak pod corn, represent perhaps the most convincing combination of evidence yet found in support of the pod-corn hypothesis.

THE EARLY EVOLUTION OF MAIZE UNDER DOMESTICATION

The Ancestral Form of Corn.—

In this paper we are concerned only with the early evolution of maize and with the evolutionary paths which it followed before the hypothetical hybridization with *Tripsacum* occurred.

If maize originated from a wild form of pod corn, then we may assume that part or all of the effects now produced by the *Tu* gene contribute toward restoring a primitive or ancestral condition. On the basis of this assumption we can conclude that:

1. Wild corn had its caryopsis enclosed in glumes.
2. The terminal inflorescence bore staminate and pistillate spikelets separately on the same branches, the former below, the latter above, as in *Tripsacum*.
3. Both staminate and pistillate spikelets were paired.
4. The plant bore no "ears" but from the upper nodes arose lateral branches, which, like the main stalk, terminated in a panicle-spike bearing staminate and pistillate spikelets.
5. It is possible, but by no means certain, that the glumes of the pistillate spikelets enclosed two functional florets.

From other evidence we can conclude that:

6. The grains of wild corn were small, flinty, and capable of popping.

There is no way of determining from the evidence (a) whether the plant was an annual or a perennial, or (b) whether branching of the stem was confined to the higher nodes or whether basal branching also occurred. I suspect, largely because there are no perennial forms of maize in existence, that wild corn was an annual.

On the question of basal branching I do not even have grounds for an opinion. Perhaps, as in present-day maize, both high branching and basal branching occurred.

It should be obvious, at least to any student of maize and its relatives, that the plant described above shows a decided resemblance to *Tripsacum*. Indeed, except for its annual habit, its membranaceous glumes, its paired pistillate spikelets, and its central spike, it is virtually identical with *Tripsacum*.

The Change From Wild Pod Corn to Modern Corn.—

If again we assume that wild maize was a form of pod corn, then it is a simple matter to visualize some of the steps involved in its evolution under domestication. Many of the changes which occurred would have been the reverse of those which now occur when the gene *Tu* is superimposed upon a modern variety. On this basis the most important event in the evolution of maize was a mutation in a single gene *Tu*. In the light of the new evidence on *Tu* alleles presented in this paper, we can no longer visualize this as a single drastic change from *Tu* to *tu* (Mangelsdorf and Reeves, 1939). Instead there must have been a series of mutations from higher to lower alleles. In either case, the ultimate effect would have been the same. The glumes became shorter. The lateral branches and their terminal inflorescences became enclosed in overlapping leaf sheaths which largely lost their leaf blades. The lateral inflorescences became pistillate, strongly compacted, and lost their basal branches until only the central spike remained. The terminal inflorescences on the main stalk, the present tassel, became wholly staminate. The caryopsis gradually became larger.

All of those changes initiated by mutations in the *Tu-tu* series which proved to be advantageous to the plant under domestication were accentuated by selection, both natural and artificial, acting upon the genes in the modifier complex so that the ultimate change was considerably greater than that produced by mutations at the *Tu* locus alone.

In following the evolutionary paths which are outlined above, maize has left upon the scene many intermediate forms. This is one important respect in which the pod-corn hypothesis differs significantly from the teosinte hypothesis. If maize originated from teosinte then the intermediate forms which must once have existed are now conspicuously lacking. True, occasional plants are found, as abnormalities, which exhibit the response to short days, characteristic of teosinte, or whose ears are distichous, or whose pistillate spikelets are single; but well-established varieties possessing these teosinte characteristics are unknown. If, on the other hand, maize originated from a wild pod corn then the intermediate forms which must have occurred are still to be found. Intermediate and weak pod forms of tunicate occur not only in prehistoric corn but also in living varieties. Varieties with elongated shanks, prominent leaf blades on the husks, and partly naked ears are common in South America. Varieties breeding true for branched ears are known in both South and Central America. Varieties in which the

development of secondary pistillate florets is the rule rather than the exception are well-known. Individual plants with mixed staminate and pistillate inflorescences are common in many varieties, especially in South America. There is apparently not a single condition intermediate between the hypothetical wild pod corn and modern, highly domesticated corn which does not still exist, usually somewhere in South America. The last fact, incidentally, is of special significance in supporting the hypothesis of a South American origin of maize.

DISCUSSION

Alphonse de Candolle in his classic "Origin of Cultivated Plants" emphasized the importance of utilizing all the evidence which can be brought to bear upon the problem involved in the origin of any particular cultivated plant and pointed out that even a combination of evidence can usually do no more than to lead to a strong probability that any given solution is correct. His conclusions regarding cultivated plants in general are particularly relevant with respect to the problem of the origin of maize, for unless maize should still be discovered actually growing in the wild, a possibility not yet ruled out, the problem of its origin may never be completely and finally solved. It may be possible, however, to accumulate a body of circumstantial evidence bearing upon the problem which will involve probabilities that approach certainty. This point perhaps has not yet been reached. On the other hand, each year of additional research yields new evidence which increases the probabilities that the pod-corn hypothesis is valid and correct and strengthens the view that maize had its origin in South America from a wild form of pod corn. The least that can be said is that the pod-corn hypothesis is no longer merely a plausible alternative to the questionable teosinte hypothesis; it has now become a valid hypothesis in its own right with an impressive body of evidence to support it. The new evidence presented in this paper, that there exists a series of alleles intermediate between *Tu* and *tu*, that intermediate and weak forms of pod corn occurred not only in prehistoric corn, but are common in living varieties of South and Central America, is perhaps the most convincing evidence in support of the pod-corn hypothesis which has yet been brought forward. Considered in the light of the evidence, old and new, summarized in this paper, it appears to me to be conclusive, at least to the extent that the burden of proof now rests upon those who question the pod-corn hypothesis or favor any alternative to it. Indeed, I feel that with the evidence now at hand we can reconstruct the ancestral form of corn with at least as much confidence in the validity of our reconstruction as paleontologists have in their reconstruction of ancestral forms of man, the horse, and other animals.

SUMMARY

1. The *Tu* gene involved in pod corn causes, in appropriate conditions, the development of (a) prominent glumes, (b) pistillate spikelets in the tassel, (c) secondary pistillate florets, (d) branching of the pistillate inflorescence, (e) elongation of the rachis, (f) elongation of the branch supporting the ear.

2. All of these effects contribute to restoring a combination of characteristics probably once primitive.

3. Two spontaneous mutations at the *Tu* locus have occurred in the course of these studies, one from *Tu* to tu^h, the other from *Tu* to *tu*. In addition, an experiment on mutability of tu^h has yielded one mutation to *tu* in a population of 2125. This corresponds to a mutation rate of 471 per million gametes.

4. A weak form of pod corn called "half-tunicate" resulting from an intermediate allele, tu^h, at the *Tu-tu* locus shows 30 per cent of crossing over with *Su* on chromosome 4.

5. Still weaker alleles of *Tu* identified by linkage and other genetic tests are common in living varieties of maize. These have their highest frequency in the maize varieties of South and Central America, and their lowest frequency in inbred strains of the United States Corn-Belt.

6. Much of the prehistoric corn of Peru and some of the prehistoric corn of the American Southwest is identical in appearance to the weak pod corn of present-day Latin American varieties and undoubtedly represents a weak form of pod corn.

7. On the assumption that maize originated from a wild form of pod corn, a reconstructed ancestral form of maize would resemble *Tripsacum* in having lateral branches arising from the nodes of the stem and terminating in panicle-spikes which bear staminate and pistillate spikelets. It would differ from *Tripsacum* in annual habit, in possessing membranaceous rather than indurated glumes, in having a central spike, and in bearing paired pistillate spikelets.

8. Forms intermediate between this hypothetical ancestral form and present-day maize varieties are common in South America.

9. The early stages of the evolution of maize under domestication, those which occurred before *Tripsacum* entered the picture, are now visualized as a series of mutations at the *Tu-tu* locus, each producing numerous morphological changes which, when advantageous under domestication, were accentuated by selection, both artificial and natural, acting upon the modifier complex.

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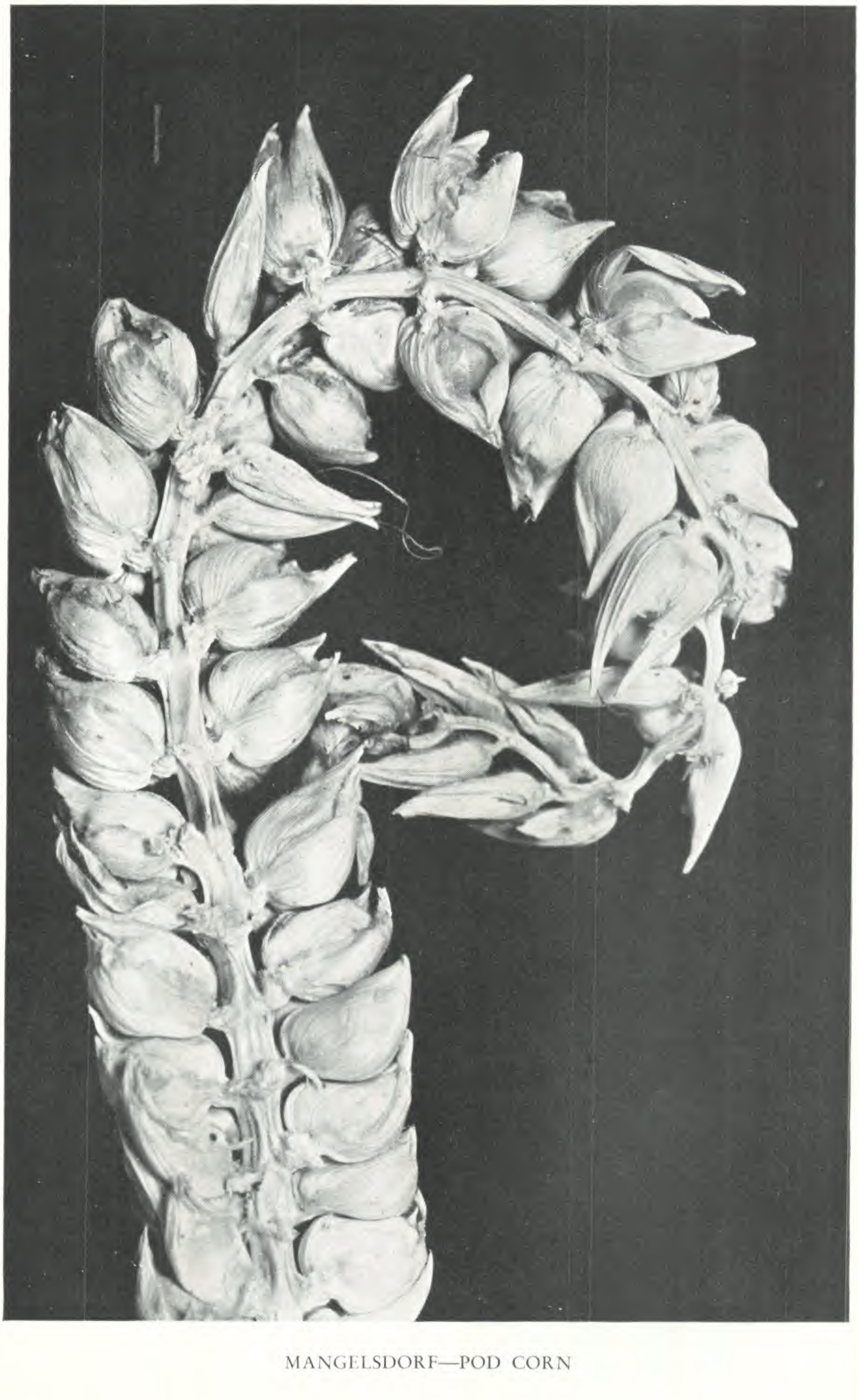
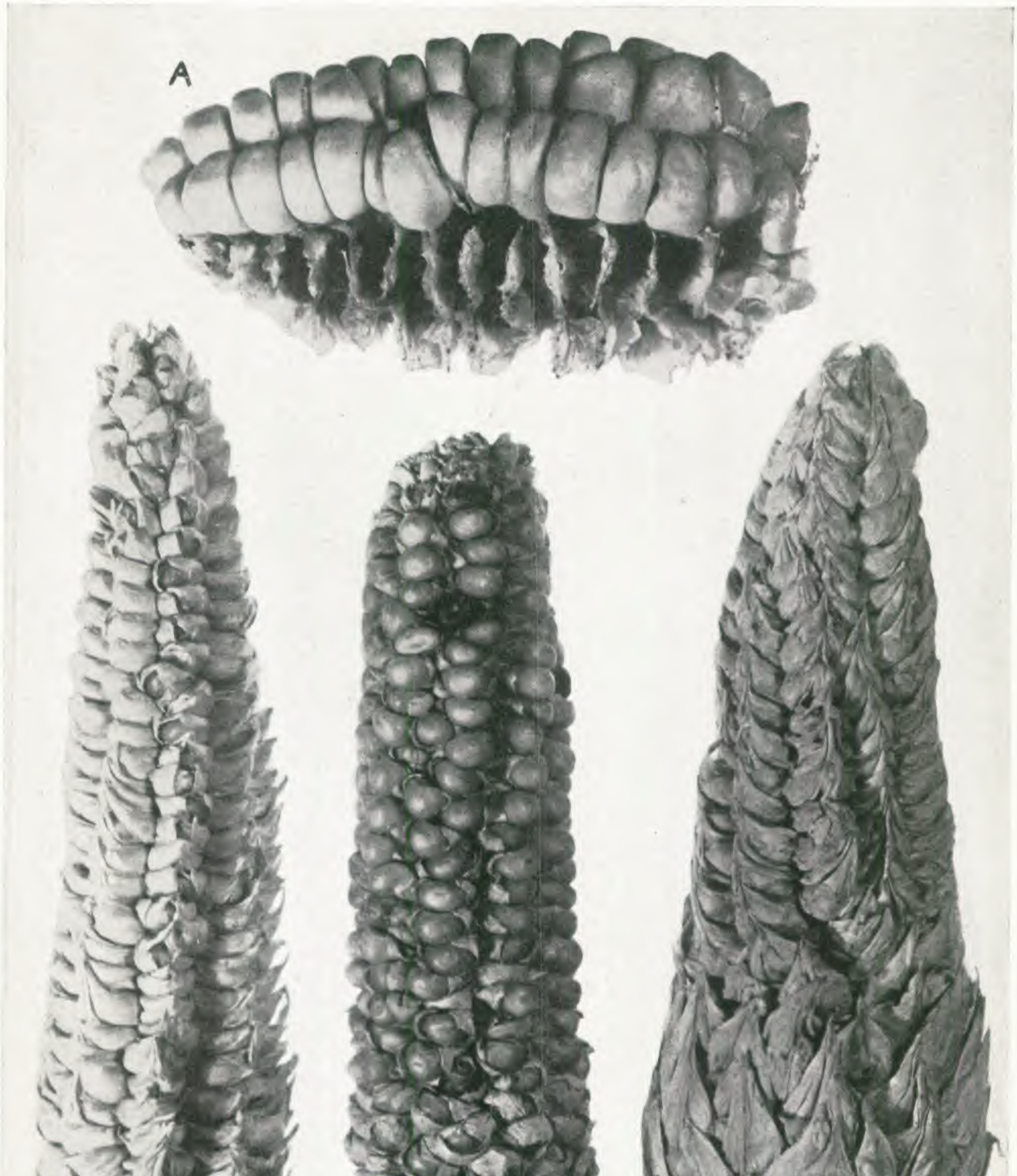
Explanation of Plate

PLATE 42

Terminal part of an ear of pod corn produced by crossing the Guarany maize of Paraguay by pod corn and backcrossing repeatedly to the Guarany parent. This ear illustrates several important characteristics of pod corn: (a) the glume-covered caryopsis; (b) the slender and fragile rachis; (c) the lack of compaction.



MANGELSDORF—POD CORN



MANGELSDORF—POD CORN

Explanation of Plate

PLATE 43

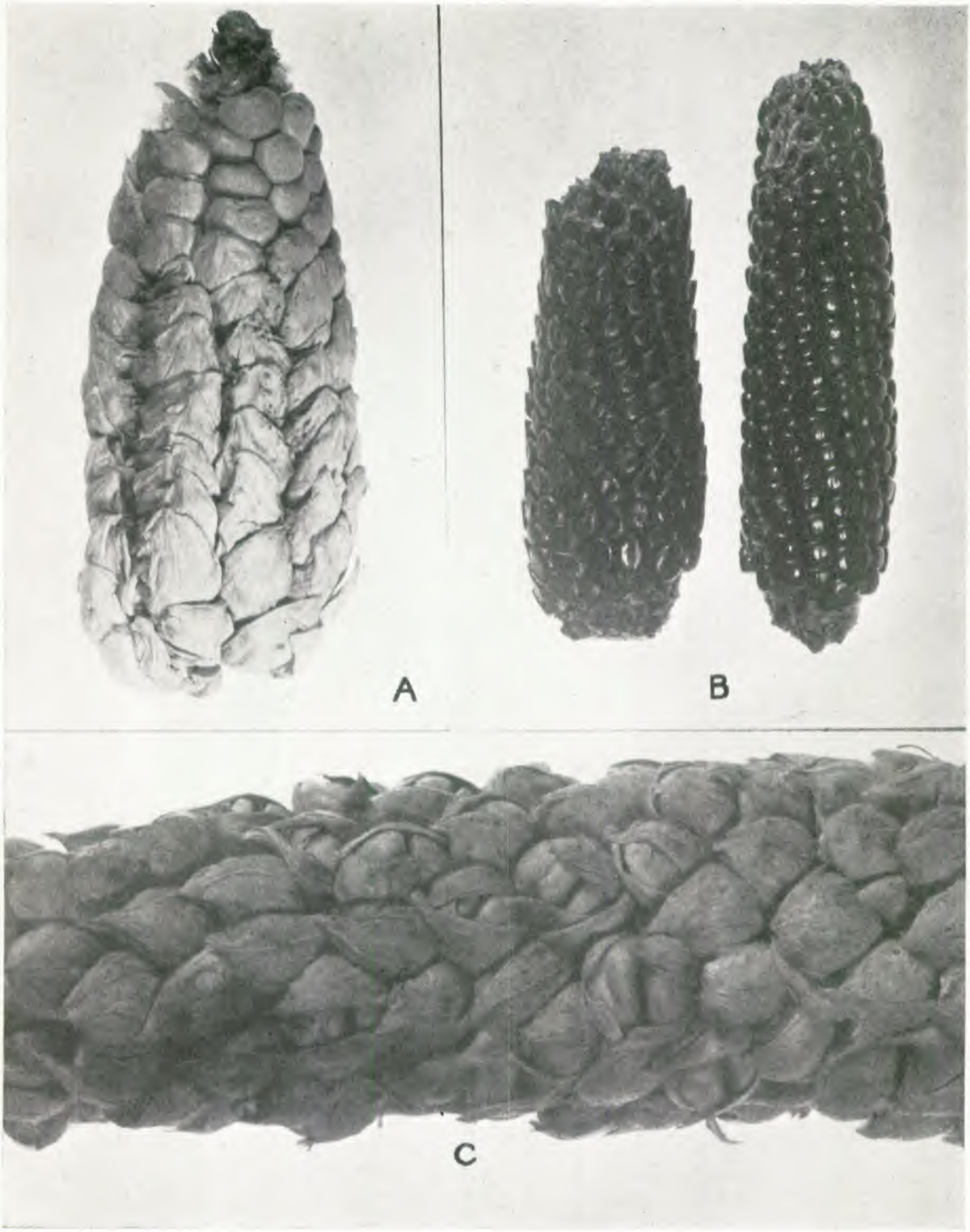
Pod corn is still well-known in South America. Ears from three countries are illustrated in this photograph. A, Peru. B and C, Bolivia. D, Brazil.

Explanation of Plate

PLATE 44

A branched ear of Guarany pod corn. It is not uncommon for ears of pod corn to be branched and this probably represents reversion to a primitive condition.

MANGELSDORF—POD CORN



MANGELSDORF—POD CORN

Explanation of Plate

PLATE 45

A. Chimera which represents a mutation from *Tu* to *tu* in somatic tissue. B. Prehistoric ears from Paracas, Peru, showing "pockets" on surface of cob, characteristic of weak pod corn. C. Portion of an ear of Guarany pod corn showing double pistillate florets, possibly a primitive condition.

EXPLANATION OF PLATE

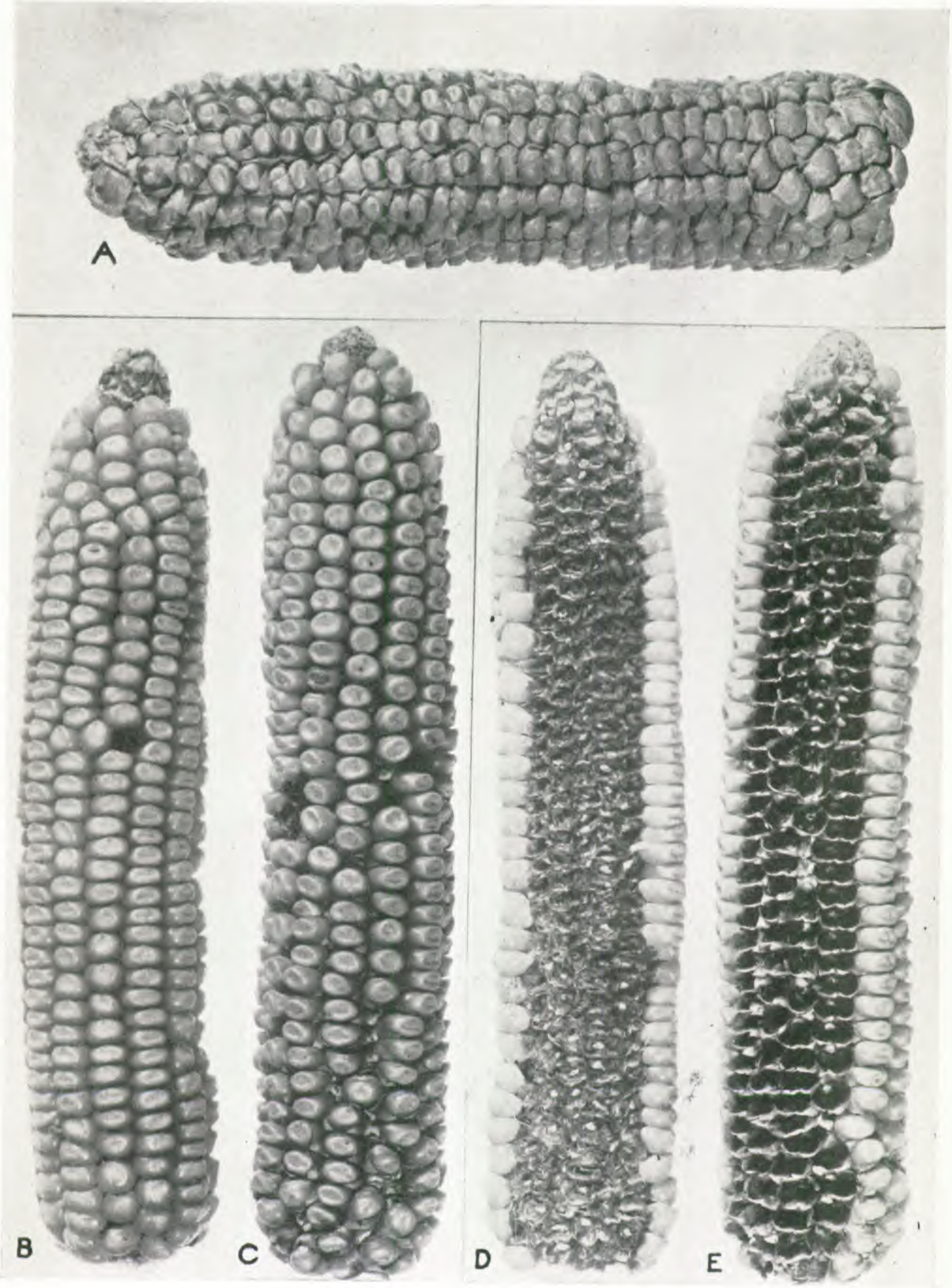
PLATE 46

A. An immature spike of tunicate teosinte showing the effect of *Tu* on the teosinte spike

B. Mature fruits from a similar spike. Note that the caryopses are completely enclosed in the glumes and that the rachis segments have become mere appendages.

C. Mature fruits of a variety of teosinte. Note that fruit cases comprise not only the glumes but also the rachis segments.

MANGELSDORF—POD CORN



MANGELSDORF—POD CORN

Explanation of Plate

PLATE 47

Ears from a relatively isogenic stock resulting from crossing and backcrossing to A158. A. An ear homozygous for tu^h. B and D. Two views of an ear homozygous for *tu*. C and E. Two views of an ear heterozygous for tu^h. Note that C which is heterozygous for half-tunicate is scarcely distinguishable from B, which is non-tunicate, until kernels are removed as in D and E. Note the alveolate surface of the cobs and the conspicuous pockets in E.

Explanation of Plate

PLATE 48

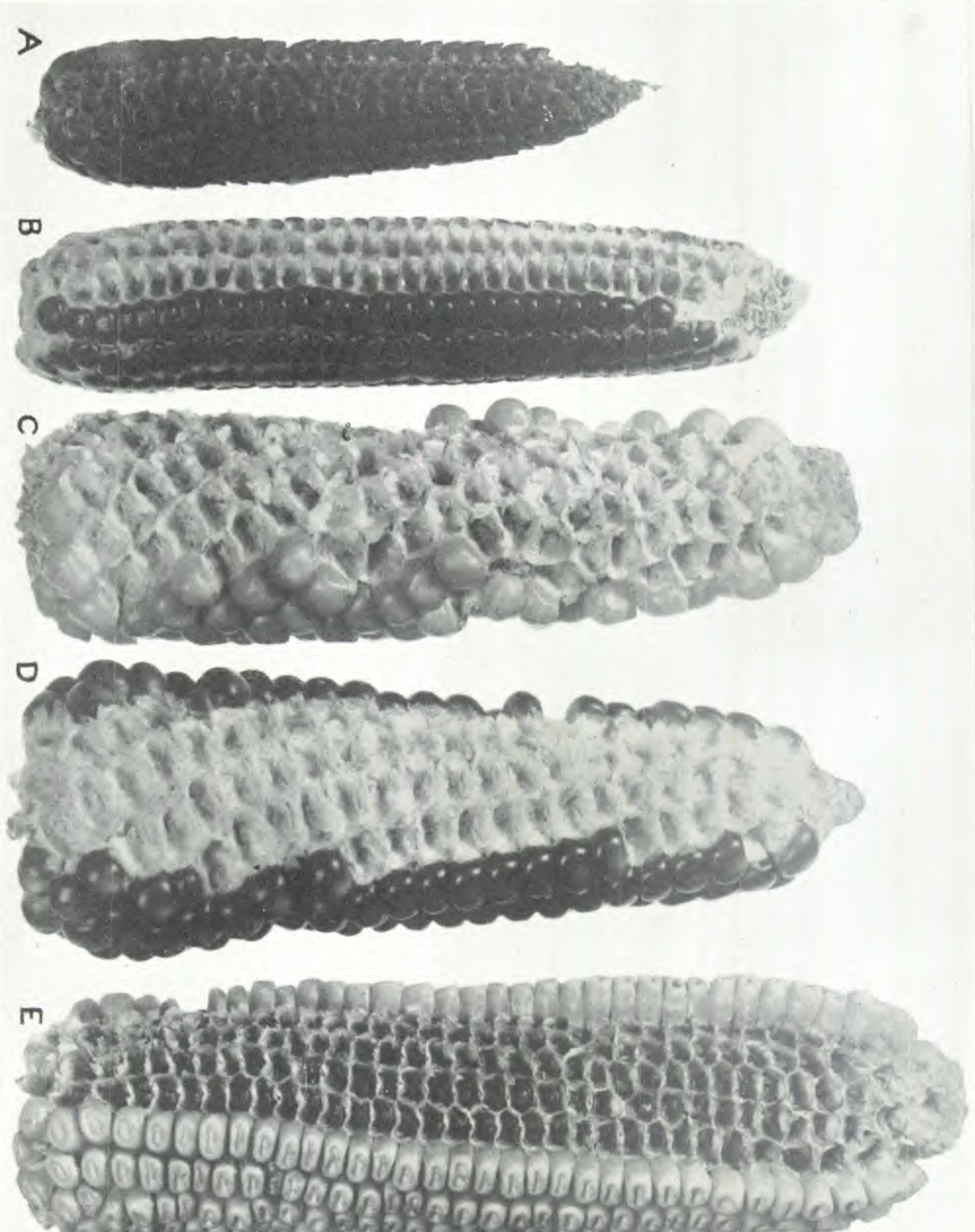
Maize varieties characterized by cobs with alveolate surfaces and conspicuous pockets and therefore probably weak pod corn.

A. Prehistoric ear from Nazca, Peru.

B. "Chapalote" maize from Mexico.

C and D. Similar ears from Colombia and Mexico, respectively.

E. An ear heterozygous for half-tunicate and therefore known to be a weak form of pod corn. Compare with ears A–D.



MANGELSDORF—POD CORN

GENERAL INDEX TO VOLUME XXXV

New scientific names of plants and the final members of new combinations are printed in **bold-face** type; synonyms and page numbers having reference to figures and plates, in *italics;* and all other matter in ordinary type.

A

Absorption spectra of epidermal cells from a Coleus leaf, 243
Acosta, Joseph de, description of maize by, 151, 153, 154
Adenocalymma bracteatum, calyx glands of, *132*
Allen, Caroline K. Lauraceae of Panama, 1
American carboniferous floras, Contributions to our knowledge of, 193
Amsonia, a new, from the Trans-Pecos, 237
Amsonia hirtella, 238; Palmeri, 238; Peeblesii, 238; **Tharpii**, 237
Anacardiaceae, living, compared with a fossil wood, 109, 110
Anderson, Edgar: and William L. Brown. A morphological analysis of row number in maize, 323; William L. Brown and. The southern dent corns, 255
Andrews, Henry N.: A note on Fomes idahoensis Brown, 207; and Robert W. Baxter. Contributions to our knowledge of American carboniferous floras. X. An Osmundaceous stem from Iowa, 193; and Sergius Mamay. A Crossotheca from northern Illinois, 203
Anemopaegma Chamberlaynii, glandular fields in leaflet of, *130*, *136;* glandular scale on, *134*
Anthocyanin concentration in hair cells of Coleus leaf, 244, 249, *252*
Apocynaceae and Asclepiadaceae, Miscellaneous new, 233
Arrabidaea Blanchetii, interpetiolar glands of, *128;* obliqua, domatia on leaflet, *130*
Asclepiadaceae, Miscellaneous new, 233

B

Bauhin, Caspar and Jean, herbals of, 165, 178; illustration of maize in, *178*
Baxter, Robert W.: A study of the vegetative anatomy of the genus Sphenophyllum from American coal balls, 209; Henry N. Andrews and. Contributions to our knowledge of American Carboniferous floras. X. An Osmundaceous stem from Iowa, 193
Beilschmiedia, 109; roxburghiana, 110
Bignoniaceae, The uses of glands in a taxonomic consideration of the family, 123
Bischofia javanica, 110
Boccone, herbal of, 178; illustration of maize in, *178*
Bock, Hieronymus, account of maize in herbal of, *152*, 156, 159
Bonnett, O. T. Ear and tassel development in maize, 269
Bridelia minutiflora, 109, 110
Brown, William L.: and Edgar Anderson. The southern dent corns, 255; Edgar Anderson and. A morphological analysis of row number in maize, 323
Brunfels' herbal, 159
Burseraceae, living, compared to a fossil wood, 109, 110

C

Callichlamys latifolia, calyx glands on leaflet of, *136*
Camerarius, account of maize in herbal of, 162, 176; illustration in, *166*
Canarium, 109; rufum, 110
Capparidaceae, 139; of Panama, 75
Carboniferous floras, Contributions to our knowledge of. X. An Osmundaceous stem from Iowa, 193
Castilla, 119
Cells, physiological activity of, 239
Ceratophytum tobagense, neuro-axillary glands of, *130*
Cleome, 139; *brachycarpa*, 143, 144; *decipiens*, 139, 142; *densiflora*, 144, *β pallens*, 144; *gracilis*, 144, *β turgescens*, 144; *hirsuta*, 144; *lateralis*, 144; *Macrothyrsus*, 144; *porphyrantha*, 144; *puberula*, 144
Coal balls, American: fossil plants in, 209; from Iowa, 193
Coleus: pigment production in hair cells, 243, *243;* absorption spectra for cells from a red and green, 244, *245-248*, *251*
Columbus's report on maize, 156
Commoner, Barry. Quantitative determination of the pigment content of single cells by means of a new microspectrophotometer, 239
Conference, the 1947, on the inflorescences of Zea Mays, 269
Contributions to our knowledge of American carboniferous floras. X. An Osmundaceous stem from Iowa, 193

Cordus, description of maize in herbal of, 160
Corn Conference of November, 1947, papers read at, 269–406
Corn: breeding, 267; cob, anatomy of, 353; embryos, Right-handed and left-handed, 317; four-rowed ear, Vascular anatomy of, 337, *340;* Indian and Turkish, *173–176;* southern dent varieties, 267
Corn, see also Maize and Zea Mays
Corn grass, 309, *310*
Corns, The southern dent, 255
Crossotheca from northern Illinois, A, 203
Crossotheca, 203; Boulayi, 204; communis, 204; Hoeninghausi, 204; **McLuckiei**, 203, *204;* pinnatifida, 204; sagittata, 204; Schartzlarensis, 204; trisecta, 204
Cruciferae of Panama, 99
Cunuria, 118
Cutler, Hugh C., and Marian C. Studies in the structure of the maize plant, 301
Cydista heterophylla, glandular fields in, *130*

D

Dent corns, the southern, 255
Dicotyledonous wood found associated with the Idaho Tempskyas, 107
Dodonaeus, description of maize in herbal of, 162, 173; illustrations of maize in, *163*
Domestication: of Hevea, 117; of maize, 394
Dothidella Ulei, 120
Durante, discussion of maize in herbal of, 165
Dwarf mutant in maize, Comparative developmental study of, 289

E

Ear and tassel in maize: development, 269, *280-286;* structure of a dwarf mutant, 289
Epidermis in Zea Mays, General features of the 341
Euphorbiaceae, living, compared to a fossil wood, 109, 110
Equisetales, relation of, to Sphenophyllum, 218
Extinction of Coleus hairs at various thicknesses, *251*

F

Ferns, fossil, 107
Finan, John J. Maize in the great herbals, 149
Flavone concentration, determination of, in Coleus hair cells, 249, *252*
Flora of Panama, Part V, Fasc. 1, 1
Fomes idahoensis Brown, A note on, 207
Food, Uses of Hevea for, in relation to its domestication, 117
Forsteronia, 236; **elachista**, 237; gracilioides, 237; **mediocris**, 237; **propinqua**, 236; spicata, 236
Fossil wood from Idaho, 108
Fossils, fern, 107, 203; in coal balls, 193, 209
Frumentum Asiaticum, 167; Indicum, 160, 167; Turcicum, 159, 167, *173*, 177
Fuchs, Leonhard, discussion of maize in herbal of, 159, 172; illustration of maize in, *158*, *161*

G

Garuga, 109; pinnata, 110
Gerarde's herbal, description of maize in, 167
Glands, The uses of, in a taxonomic consideration of the family Bignoniaceae, 123
Gómara, description of maize by, 153
Gramineae, epidermis in the, 341
Guilielma Gasipaes, 119
Gynandropsis, 139, 141; *adenocarpa*, 144; *aurantiaca*, 143; *brachycarpa*, 140, 143; *chiriquensis*, 142; *coccinea*, 143; *decipiens*, 142; *densiflora*, 144; *gracilis*, 145; *hirsuta*, 144; *hispidula*, 143; *Jamesonii*, 144; *lateralis*, 144; *macrophylla*, 145; *macrothyrsus*, 144; *Mathewsii*, 144; *orba*, 145; *pentaphylla*, 139; *porphyrantha*, 145; *phoenicea*, 144; *puberula*, 144; *pulcherrima*, 143; *Ulei*, 144

H

Herbals, great, Maize in the, 149; passages from original texts quoted and translated, 187; woodcuts of, 179, 184
Hernández, description of maize by, 165
Hernandiaceae of Panama, 68
Hevea, The uses of, for food in relation to its domestication, 117
Hevea pauciflora, 120

I

Idaho: coniferous wood found near Wayan, 107; Fomes idahoensis Brown from, 207
Illinois: coal balls from, 204; A Crossotheca from northern, 203
Inflorescence of Zea Mays, 269-406
Iowa, An Osmundaceous stem, from, 193

J

Jacaranda mimosiflora, capitate glandular hairs on staminodium of, *136*

K

Kirkia acuminata, 109, 110
Koordersiodendron, 109; pinnatum, 110

L

Laubengayer, R. A. The vascular anatomy of the four-rowed ear of corn, 337
Lauraceae: living, compared with a fossil wood, 110; of Panama, 1
Lenz, Lee Wayne. Comparative anatomy of the female inflorescence of Zea Mays L., 353
Light, relation of, to cell investigation, 239
l'Obel, see Obel
Lundia corymbifera, interpetiolar gland on stem of, *134*

M

Mahiz, 153
Maize, see also Corn and Zea Mays
Maize: anatomy of female inflorescence of, 353; Caribbean, 183; cob, 304, 353; colors of kernels according to herbalists, 169; domestication of, 394; dwarf mutant in, 289; ear and tassel development in, 269; epidermis in, 341; evolution of, 377; flints, 182; four-rowed ear, 337; history of, 149, 180, 255; in the great herbals, 149, illustrations, *150–175*; in post-conquest Hispanic America, 150; names in herbals for, 168; origin of, 397; place of origin according to herbals, 169; pod corn, role of, in origin of maize, 377; religious ceremonies connected with, 155; row number in ears, 323, 337; southern dent varieties, 255, *268*; structure of, 289, 301; tassel and ear development, 269
Malouetia **Quadricasarum**, 234; tamaquarina, 235; Schomburgkii, 235
Mamay, Sergius, Henry N. Andrews and. A Crossotheca from northern Illinois, 203
Mandevilla **longipes**, 233; *subsagittata*, 234; **turgida**, 234; *Vanheurckii*, 234
Mangelsdorf, Paul C. The role of pod corn in the origin and evolution of maize, 377
Manisuris cylindrica, 302, *311*
Matelea **purpureolineata**, 237
Matthiolus, description of maize in herbal of, 163, 164; illustration of maize in, *156*
Mauria simplicifolia, 110
Memora Klugii, corolla glands of, *132*
Mespilodaphne sassafras, 110
Microspectrophotometer, a new: optical diagram of, *240*; Quantitative determination of the pigment content of single cells by means of, 239
Milium indicum, 162
Miscellaneous new Apocynaceae and Asclepiadaceae, 233
Monardes, description of maize in herbal of, 165
Morangaceae of Panama, 75
Morleya, 233; **leipocalyx**, 233
Mutant in maize, a dwarf, 289

N

Neuropteris, 204

O

l'Obel, herbal of, 162, 176; illustration of maize in, *163*
Origin and evolution of maize, Role of pod corn in, 377
Osmundaceae, 193
Osmundaceous stem from Iowa, 193
Osmundites, 195; Dowkeri, 195; Dunlapi, 195; Kolbei, 195; Schemnitzensis, 195; skidegatensis, 196
Oviedo's "Historia natural y general," 150; description of maize in, 151, 154, 164; illustration of maize in, *150*

P

Pachyptera Kerere, interpetiolar and petiolar glands of, *128*
Paleobotanical studies, 107, 193, 203, 207, 209
Panama, Flora of, Part V, Fasc. 1 (Lauraceae to Cruciferae), 1
Papaveraceae of Panama, 71
Paraphyllanthoxylon arizonense, 108; **idahoense**, 108, *112*, *115*
Parkinson, John, discussion of maize in herbal of, 167
Pecopteris, 203, 204
Pedicellaris, 139; *Lehmannii*, 144; *Ulei*, 144
Petitia domingensis, 110, 111
Phyllanthus emblica, 109, 110
Pigment content of single cells, Quantitative determination of, by means of a new microspectrophotometer, 239
Plumeria, 233
Pod corn, Role of, in the origin and evolution of maize, 377
Podandrogyne, 139, 141; **brachycarpa**, 143; **cernua**, 143; chiriquensis, 142, *146*; **coccinea**, 143, *146*; **decipiens**, 142; glabra, 141, 145; **gracilis**, 144; **macrophylla**, 145; *orba*, 145; **polychroma**, 145; *pubescens*, 145

Polypore, A fossil, from Idaho, 207
Prat, Henri. General features of the epidermis in Zea Mays, 341
Prestonia didyma, 236; **Haughtii**, 235; **macrophylla**, 235; obovata, 236
Protoosmundites Wilsonii, 194, *198*, *201*
Pseudocalymma sp., interpetiolar glands of, *128*
Pteridosperm stems in Iowa coal balls, 193

Q

Quantitative determination of the pigment content of single cells by means of a new microspectrophotometer, 239

R

Religious ceremonies, maize in, 155
Rhodea, 204
Right-handed and left-handed corn embryos, 317
Rollins, Reed C. Cruciferae of Panama, 99
Row number in maize, A morphological analysis of, 323

S

Schery, Robert W., Robert E. Woodson, Jr., and, and collaborators. Flora of Panama. Part V, Fascicle 1 (Lauraceae to Cruciferae), 1
Schinopsis balansea, 110
Seibert, R. J.: The use of glands in a taxonomic consideration of the family Bignoniaceae, 123; The uses of Hevea for food in relation to its domestication, 117
Simarubaceae, living, compared to a fossil wood, 109, 110
Siphonia, 118
Southern dent corns, 255, *268*; chromosome knobs, 257, *258*; internode diagram, *260*, *261*; old southern dents, 262; derived varieties, 263
Spackman, William, Jr. A dicotyledonous wood found associated with the Idaho Tempskyas, 107
Spectrophotometric measurements, determination of anthocyanin and flavone concentration in cells by, 239, *242*
Sphenophyllum, Vegetative anatomy of, 209
Sphenophyllum, 209; Dawsoni, 209; Gilkineti, 210, 218; insigne, 210, 217; minus, 218; perforatum, 210, 217; plurifoliatum, 210, 217, *220–231*
Sphenopteris 203
Staphylopteris sagittatus, 204
Stem remains of ferns in coal balls, 193
Stephens, S. G. A comparative developmental study of a dwarf mutant in maize and its bearing on the interpretation of tassel and ear structure, 289

T

Tassel in maize: development of, 269, *280-286*; structure of, in a dwarf mutant, 289
Tempskyas, Idaho, A dicotyledonous wood found associated with, 107
Tabernaemontanus' herbal, description of maize in, 160, 177; illustrations of maize in, *173–177*
Teopod maize ear, 310, *310*
Teosinte, 302, *311*, 317
Thamnopteris, 196; Schlechtendalii, 196
Tlaolli, 165
Tovariaceae of Panama, 75
Tripsacum, 302, *311*
Triticum Bactrianum, 160; Turcicum, 162

U

Urticaceae, 111

V

Vascular anatomy of the four-rowed ear of corn, 337
Verbenaceae, living, compared to a fossil wood, 110

W

Weatherwax, Paul. Right-handed and left-handed corn embryos, 317
Welschen Korn, 156
Woodcuts: botanical, 185; copying, 186; historical background of, 184; of maize in the herbals, 170, 179
Woodson, Robert E., Jr.: Gynandropsis, Cleome, and Podandrogyne, 139; Miscellaneous new Apocynaceae and Asclepiadaceae, 233; and Robert W. Schery and collaborators. Flora of Panama. Part V, Fascicle 1 (Lauraceae to Cruciferae), 1

Z

Zalesskya, 195; diploxylon, 196; gracilis, 196
Zea Mays—See Corn and Maize
Zea Mays L., Comparative histology of the female inflorescence of, 353; General features of the epidermis in, 341
Zea mexicana, 302

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Annals
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Special number,
"The 1947 Conference on the Inflorescences of *Zea Mays*"

Ear and Tassel Development in Maize . . . . . . O. T. Bonnett 269–287
A Comparative Developmental Study of a Dwarf Mutant in Maize, and Its Bearing on the Interpretation of Tassel and Ear Structure . . . . S. G. Stephens 289–299
Studies on the Structure of the Maize Plant . . . . Hugh C. Cutler and Marian C. Cutler 301–316
Right-handed and Left-handed Corn Embryos . Paul Weatherwax 317–321
A Morphological Analysis of Row Number in Maize . . . . Edgar Anderson and William L. Brown 323–336
The Vascular Anatomy of the Four-rowed Ear of Corn . . . . R. A. Laubengayer 337–340
General Features of the Epidermis in *Zea Mays* . . Henri Prat 341–351
Comparative Histology of the Female Inflorescence of *Zea Mays* L. . . . . Lee W. Lenz 353–376
The Role of Pod Corn in the Origin and Evolution of Maize . . . . Paul C. Mangelsdorf 377–406
General Index to Volume XXXV 407–410

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THE 1947 CONFERENCE ON THE INFLORESCENCES OF *ZEA MAYS*

The inflorescences of *Zea Mays* (corn ears and corn tassels in common speech) are without parallel in the plant kingdom for the complexity of their structure and the multiformity of their variability. There is still no general agreement among botanists as to the phylogeny of these organs nor as to their morphological interpretation.

In the last decade new evidence bearing on these problems has been produced in various laboratories and by various techniques. A conference was held at the Missouri Botanical Garden on November 8, 1947, to which those known to be working on the subject were invited. The conference sessions were devoted to a series of informal discussions and demonstrations. One of the results of that conference is this series of interrelated papers. They not only present new data—they demonstrate new techniques and extensions of old ones and bring into juxtaposition facts previously considered unrelated.

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